

FINAL REPORT
Northwest Climate Science Center Funded Project

1. ADMINISTRATIVE:

Project Title: Predicting Climate Change Impacts on River Ecosystems and Salmonids across the Pacific Northwest: Combining Vulnerability Modeling, Landscape Genomics, and Economic Evaluations for Conservation

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2. PUBLIC SUMMARY:

Salmonids – a group of coldwater adapted fishes of enormous ecological and socio-economic value – historically inhabited a variety of freshwater habitats throughout the Pacific Northwest (PNW). Over the past century, however, populations have dramatically declined due to habitat loss, overharvest, and invasive species. Consequently, many populations are listed as threatened or endangered under the U.S. Endangered Species Act. Complicating these stressors is global warming and associated climate change. Overall, aquatic ecosystems across the PNW are predicted to experience increasingly earlier snowmelt in the spring, reduced late spring and summer flows, increased winter flooding, warmer and drier summers, increased water temperatures, and expansion of invasive species. Understanding how effects of climate change might influence habitat for native salmonid populations is critical for effective management and recovery of these species. Scientists at the USGS and University of Montana used novel techniques and empirical data to study how climate change may drive landscape scale impacts that affect freshwater habitats and populations of key salmonid species (bull trout, cutthroat trout, and steelhead) throughout the PNW. Results showed strong linkages between climatic drivers – temperature and flow regimes – and the distribution, abundance and genetic diversity of native salmonids across the PNW. Specifically, warming temperatures and shifting flow regimes are expected to fragment stream systems and cause salmonids to retreat upstream to headwater areas, thereby decreasing fish population abundance and genetic diversity – both of which are critical for persistence in a changing landscape. Climate-change-induced periods of decreasing spring snowmelt and increases in stream temperatures are likely to decrease native biodiversity by fostering cross-breeding between invasive and native trout species. The study also developed a new framework for assessing the vulnerability of freshwater species to climate change and other stressors in complex stream networks, which will aid managers in pro-actively implementing conservation programs to increase resiliency and adaptive capacity of aquatic species.

3. TECHNICAL SUMMARY:

Climate change is increasingly threatening the biodiversity of aquatic ecosystems worldwide (Walther et al. 2002, Parmesan and Yohe 2003, Isaak et al. 2012). Combined with additional stressors, such as habitat loss and invasive species, these changes are likely to shift patterns of distribution, abundance, phenology, and genetic diversity in many species (Parmesan 2006). This is particularly true

for many aquatic species restricted to stream environments with spatial gradients in temperature, flow, and physical habitat conditions. Understanding how species and habitats are likely to respond to climate warming is critical in developing effective conservation and management strategies for freshwater systems. Climate change is expected to dramatically impact the structure and function of freshwater ecosystems and salmonid species, yet no study has comprehensively assessed these impacts across Pacific Northwest (PNW) riverscapes. Salmonids are “keystone” species for both aquatic and terrestrial ecosystems, and serve as excellent indicators of ecosystem health in the face of climate change since they are ectothermic and highly sensitive to warm temperatures and modified flow regimes. They also contribute enormously to regional economies and Native American cultures. The evolutionary consequences of climate change are one of our greatest areas of uncertainty because empirical data addressing this issue are extraordinarily rare. This research expanded on existing climate change research projects focused on how hydrologic, thermal, and habitat change influences native salmonids (threatened bull trout, steelhead, and westslope cutthroat trout) in the PNW. The project applied new techniques for combining spatially downscaled climate data with fine-scale salmonid species vulnerability assessments, population genetic data, and remotely sensed riparian and aquatic habitat analyses. Results identify populations, species, habitats, and ecosystems most susceptible to the impacts of climate change, design long-term monitoring programs, estimate potential economic consequences, inform future research needs, and develop conservation delivery options in response to climate change and other important cumulative stressors (e.g., habitat loss).

Here, we developed a novel interdisciplinary modeling framework to predict how climate change will influence riverscape connectivity, population vulnerability, and adaptive potential of ecologically important species and riverscapes. For “technology transfer”, this project combined species’ distributions, population demographic and genomic data, landscape genetic models, climate change models of habitat quality and connectivity (water flow, temperature) to predict vulnerability of stream reaches (~1 km scale) and salmonid populations to climate change by 2040 and 2080. This project also produced predictive models and maps relevant to fish and habitat management that identify vulnerable populations, river segments, and ecosystems at multiple spatial scales across the PNW. To date, we have published four articles in peer reviewed scientific journals and two more are currently in review. Overall, this study is a tremendous step forward in our understanding of how climate change can influence evolutionary process and ultimately species biodiversity across the PNW.

Major scientific results and advancements from this project include:

- Rapid climate warming can exacerbate interactions between native and non-native trout species through invasive hybridization (Muhlfeld et al. 2014).
- Climate-change-induced stream temperature increases that restrict movements and further reduce suitable habitats to headwater streams are likely to fragment habitat networks, thereby decreasing fish population abundance and genetic diversity, both of which are critical for persistence (Muhlfeld et al. 2014; Landguth et al. 2014; Kovach et al. 2015; Wade et al. In-prep).
- Watersheds containing threatened bull trout populations with lower average genetic diversity generally had the lowest habitat complexity, warmest stream temperatures, and greatest frequency of winter flooding. Together, these findings have important conservation implications for bull trout and other imperiled species because genetic diversity is already depressed where climatic vulnerability is highest and is predicted to likely erode further in the very places where diversity may be most needed for future persistence (Kovach et al. In-press).
- Riverscape and climatic variables shape the genetic structure of steelhead populations across the PNW. However, we highlight the need for caution when extrapolating results from one study area to another (Hand et al. In-review).
- We introduce a novel modeling framework for aquatic systems that integrates spatially explicit, individual-based, demographic and genetic (demogenetic) assessments with environmental variables to assess species' vulnerability to climate change and human stressors (Landguth et al. 2014).
- Multispecies climate change vulnerability assessments (CCVAs) offer the ability to relatively rank and prioritize populations of multiple sympatric species. However, CCVAs often neglect crucial sources of adaptive potential (genetic diversity) combined with environmental and demographic data. For bull trout and steelhead, we showed that the failure to consider a more robust set of metrics might lead to greatly differing vulnerability rankings for independent watersheds. This has major implications for management decisions that often rely on one or two sources of data, and potentially lead to incomplete, or incorrect assumptions when it comes to prioritizing

population vulnerability (Wade et al. In-prep).

- We developed and described a novel framework to aid future conservation research and management by offering a more holistic treatment of interacting species and the abiotic environment in which those interactions take place. This landscape community genomics (LCG) framework is based on the important observation that genomic variation is strongly influenced by complex and dynamic interactions between environmental and community effects. Failure to consider both effects on evolutionary dynamics simultaneously can lead to incomplete, spurious, or erroneous conclusions about the mechanisms driving genomic variation and thus negatively impact conservation management decisions (Wade et al. In-prep).
- This project improved the Riverscape Analysis Project (RAP; <http://rap.ntsg.umn.edu>). The RAP decision support system offers a new and powerful web-based platform to aid conservation practitioners by better educating them on and empowering them with cutting-edge web-tools and “best” practices in CCVAs. Further, the RAP DSS allows managers to save on precious time and money resources by offering a user-friendly interface to 1) download an extensive database of environmental (e.g., physical riverscape features and climate) data, 2) directly apply environmental data with demographic and genetic data to conduct pilot CCVAs.
- Future climate warming is predicted to have substantial socio-economic impacts in freshwater ecosystems. We demonstrated a way to link ecological metrics from climate change impacts on natural systems to a model of an economically important human system, sportfishing in Montana. The primary finding is that the increasing absence of cutthroat trout (modeled at years 2059 and 2099 and interpolated from a year 2000 baseline) and a 50% reduction in trout biomass in the Upper Flathead would have a present value loss of \$116 million in 2010 dollars. The work to date is more of a proof of concept than a definitive empirical estimate, and is likely to be quite a conservative estimate. It would be feasible to use these types of estimates to inform management and conservation decisions, such as evaluating the cost effectiveness of controlling source populations of invasive species (e.g. rainbow trout) to protect the remaining cutthroat populations in these systems.

4. PURPOSE AND OBJECTIVES:

Accelerating climate change and other cumulative stressors create an urgent need to understand the influence of environmental variation and landscape features on the connectivity and vulnerability of freshwater fish species. The overall goal of this project was to determine effects of climate change on native salmonid (bull trout, westslope cutthroat trout, and steelhead) habitats and population vulnerability by linking climatic data and remotely-sensed measures of freshwater physical habitat complexity with dynamic, spatiotemporal models of population abundance, connectivity, and genomic diversity. A second goal was to provide novel web based tools for managers and decision makers to easily understand and visualize effects of climate change on river ecosystems and salmonid vulnerability.

The objectives of this project were to:

- **Objective 1:** Assess how climate change influences invasive hybridization in native trout
- **Objective 2:** Combine demographic and genetic factors to assess population vulnerability in stream species
- **Objective 3:** Assess how climatic variation and vulnerability is related to genetic diversity of threatened bull trout throughout the PNW
- **Objective 4:** Assess how climate and habitat characteristics influence genetic diversity of steelhead across the PNW
- **Objective 5:** Assess the vulnerability of steelhead and bull trout to climate change effects across the PNW
- **Objective 6:** Explore, conceptualize and develop a framework that applies a more holistic, landscape community genomic approach to help advance conservation science and management.

- **Objective 7:** Assess potential socioeconomic impacts of potential climate warming on cutthroat trout.

5-9. ORGANIZATION AND APPROACH/RESULTS/ANALYSIS AND FINDINGS/CONCLUSIONS and RECOMMENDATIONS/MANAGEMENT APPLICATIONS AND PRODUCTS

This section of the report provides details for these sections by objective.

Objective 1: Assess how climate change influences invasive hybridization in native trout

Muhlfeld, Clint C., Ryan P. Kovach, Leslie A. Jones, Robert Al-Chokhachy, Matthew C. Boyer, Robb F. Leary, Winsor H. Lowe, Gordon Luikart, and Fred W. Allendorf. 2014. **Invasive hybridization in a threatened species is accelerated by climate change.** *Nature Climate Change* 4:620-624.
DOI:10.1038/nclimate2252.

Summary

*Climate change will decrease worldwide biodiversity through a number of potential pathways, including invasive hybridization (i.e., cross-breeding between invasive and native species). How climate warming influences the spread of hybridization and loss of native genomes poses difficult ecological and evolutionary questions with little empirical information to guide conservation management decisions³. Here we combine long-term genetic monitoring data with high resolution climate and stream temperature predictions to evaluate how recent climate warming has influenced the spatiotemporal spread of human-mediated hybridization between threatened native westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) and non-native rainbow trout (*Oncorhynchus mykiss*), the world's most widely introduced invasive fish. Despite widespread release of millions of rainbow trout over the past century within the Flathead River system, a large relatively pristine watershed in Western North America, historical samples revealed that hybridization was only prevalent in one (source) population. During a subsequent 30-year period of accelerated warming, hybridization spread rapidly and was strongly linked to interactions between climatic drivers—precipitation and temperature—and distance to the source population. Specifically, decreases in spring precipitation and increases in summer stream temperature*

likely promoted upstream expansion of hybridization throughout the system. This study shows that rapid climate warming can exacerbate interactions between native and non-native species through invasive hybridization, which could spell genomic extinction for many species.

Purpose and Objectives

Changes in species ecology associated with climate change have been documented for a broad range of organisms, yet empirical understanding of how climate change influences evolutionary processes and resulting patterns of biodiversity is limited. One consequence of climate-induced range shifts is increased sympatry between previously isolated species, potentially resulting in introgressive hybridization (i.e., genes from an invasive species spread into a native species). Salmonids—a group of fishes of enormous ecological and socioeconomic value—are ideal organisms for examining how climate change facilitates hybridization between native and non-native species. Quantifying spatial and temporal genetic changes in wild populations, including introgression, provides strong support for climate-induced evolutionary change. Such data, however, are limited among vertebrates, especially for rare and endangered species.

In this study, we used long-term genetic monitoring data (1978-2008) to test the prediction that climatic variation has affected the spread of introgressive hybridization between threatened native westslope cutthroat trout and non-native rainbow trout. Specifically, we tested the prediction that increased summer stream temperatures, decreased spring precipitation, and wildfire disturbance have influenced the spatiotemporal spread of hybridization throughout the Flathead River system (USA and Canada).

Approach

Historical (1978-1984) samples were genotyped at six species diagnostic allozyme loci. Recent (2000-2008) samples from the 21 historically sampled populations and an additional 29 populations throughout the basin were genotyped at seven diagnostic microsatellite loci. Linear models and Akaike's Information Criterion (AIC) were used to test for relationships between variables hypothesized to influence introgression and to select the best-supported models. Specifically, we tested whether biotic and climatic variation were related to the amount of rainbow trout hybridization across sites ($N = 50$) and over time based on repeat samples from the late 1970s and early 1980s and early 2000s ($N = 20$ sites; the source population was not included in the model).

Predictor variables for each population included flow-connected stream distances to the source of rainbow trout, spring precipitation (April, May, June, and three month average), summer stream temperature, and the presence or absence of recent wildfire (since 1984) within each stream drainage. Covariates were obtained for each location using ArcGIS version 10.1 (Environmental Systems Research Institute, Redlands, California, USA). Average summer stream temperature conditions were predicted using a spatially explicit stream temperature model for the Flathead River basin driven by high-resolution air temperature surfaces (800 m). Average precipitation conditions were calculated from daily precipitation surfaces (1 km) processed from National Aeronautics and Space Administration (NASA) Daymet data.

Results

Genetic samples collected from the late 1970s and early 1980s detected low levels (<2%) of hybridization in just 2 of 20 sites, and a hybrid swarm (representing multiple generations of hybridization) with a predominant (92%) genetic contribution from rainbow trout was discovered in the lower valley in 1994 (Fig. 1a). Conversely, samples from the 2000s showed introgression in 9 of the 18 previously non-hybridized sites, demonstrating that introgression increased rapidly over a 30-year period (from 10% to 52% of all sites; Fig. 1b).

Climatic factors, including May precipitation (representing the timing and magnitude of spring streamflow and summer stream temperature, were strongly related to the extent of hybridization occurring over geographic space (Fig. 1, Table 1). An interaction effect between May precipitation and proximity to the historic source of rainbow trout best explained hybridization levels across the stream network (Table 1; $R^2 = 0.81$). Introgression was substantially greater in populations where May precipitation was low (<2 cm), mean stream temperatures were >10°C, and the source population was within 90 km (Fig. 1). The best-supported model explaining temporal change in introgression also included an interaction between changes in precipitation and distance to source (Table 1), where the greatest increases in hybridization occurred at locations near the source and with the greatest decreases in precipitation. Finally, there was strong evidence that an interaction between stream temperature and precipitation best explained introgression after correcting for distance ($P < 0.001$).

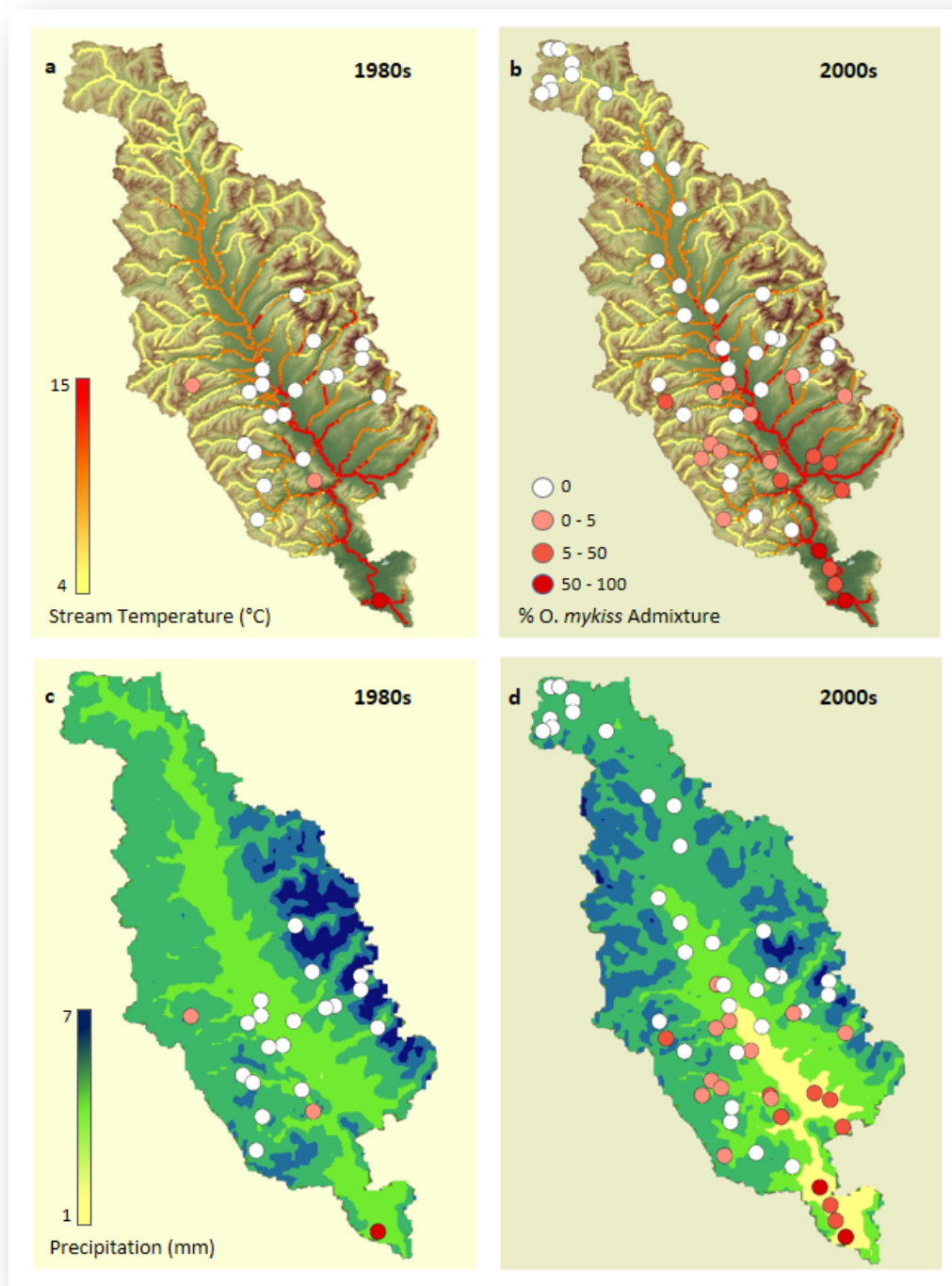


Fig 1. Spatiotemporal spread of hybridization related to stream temperature and spring precipitation.

Conclusions

We found that climatic drivers and human-mediated introductions of an invasive species have interacted to increase introgressive hybridization in nature. The rapid spread of rainbow trout hybridization was likely driven by an earlier peak and decrease in magnitude of spring streamflow. Periods of reduced spring flooding and flows have likely allowed rainbow trout to proliferate and hybridize with native cutthroat trout populations. Summer water temperature was also related to the extent of hybridization, but to a lesser degree, likely due to its direct relationship with spring precipitation and summer baseflow.

Aquatic ecosystems in Western North America are predicted to experience increasingly earlier snowmelt in the spring, reduced late spring and summer flows, warmer and drier summers, and increased water temperatures. Although regional spring precipitation is projected to increase, which may buffer these trends, periods of reduced and earlier spring precipitation (e.g., drought) will significantly exacerbate these conditions. These climatic changes threaten to erode native trout genomes as rainbow trout continue to expand their range through climate-induced “windows of opportunity”, putting many extant populations at greater risk than previously thought.

Many native salmonids are already at risk of climate-induced extirpation due to physiological requirements for cold temperatures, combined with historic population declines from a century of intensive habitat alterations and species introductions. Our findings underscore the negative consequences of climate change for native trout and other species threatened by human-mediated hybridization, as well as the potential for both ecological and evolutionary impacts on biodiversity.

Management implications

We found that hybridization can rapidly spread as invasive species expand their range due to perturbations in climatic conditions, with irreversible evolutionary consequences for threatened species. Protecting genetic integrity and diversity—critical for long-term resiliency in the face of environmental change—will be incredibly challenging when species are threatened with climate-induced invasive hybridization. Conservationists will be increasingly confronted by a double-edged sword: protect native genomic integrity via isolation management at the cost of losing genetic and life history diversity, or allow introgression to proceed, causing extinction of native genomes that have evolved over millennia. While hybridization may increase genetic diversity for some species, and thus adaptive potential, genomic extinction appears imminent for cutthroat trout if hybrid source populations are not

eliminated. Climate change will, thus, pose complex and, at present, relatively underappreciated dilemmas for biodiversity protection in the future.

Objective 2: Combining demographic and genetic factors to assess population vulnerability in stream species

Erin L. Landguth, Clint C. Muhlfeld, Robin S. Waples, Leslie Jones, Winsor H. Lowe, Diane Whited, John Lucotch, Helen Neville, and G. Luikart. 2014. **Combining demographic and genetic factors to assess population vulnerability in stream species.** *Ecological Applications* 24:1505-1524.

Summary

*Accelerating climate change and other cumulative stressors create an urgent need to understand the influence of environmental variation and landscape features on the connectivity and vulnerability of freshwater species. Here, we introduce a novel modeling framework for aquatic systems that integrates spatially explicit, individual-based, demographic and genetic (demogenetic) assessments with environmental variables. To show its potential utility, we simulated a hypothetical network of 19 migratory riverine populations (e.g., salmonids) using a riverscape connectivity and demogenetic model (CDFISH). We assessed how stream resistance to movement (a function of water temperature, fluvial distance, and physical barriers) might influence demogenetic connectivity, and hence, population vulnerability. We present demographic metrics (abundance, immigration, and change in abundance) and genetic metrics (diversity, differentiation, and change in differentiation), and combine them into a single vulnerability index for identifying populations at risk of extirpation. We considered four realistic scenarios that illustrate the relative sensitivity of these metrics for early detection of reduced connectivity: (1) maximum resistance due to high water temperatures throughout the network, (2) minimum resistance due to low water temperatures throughout the network, (3) increased resistance at a tributary junction caused by a partial barrier, and (4) complete isolation of a tributary, leaving resident individuals only. We then applied this demogenetic framework using empirical data for a bull trout (*Salvelinus confluentus*) metapopulation in the upper Flathead River system, Canada and USA, to assess how current and predicted future stream warming may influence population vulnerability. Results suggest that warmer water temperatures and associated barriers to movement (e.g., low flows, dewatering) are predicted to fragment suitable habitat for migratory salmonids, resulting in the loss of genetic diversity and reduced*

numbers in certain vulnerable populations. This demogenetic simulation framework, which is illustrated in a web-based interactive mapping prototype, should be useful for evaluating population vulnerability in a wide variety of dendritic and fragmented riverscapes, helping to guide conservation and management efforts for freshwater species.

Purpose and Objectives

Climate change is increasingly threatening the biodiversity of aquatic ecosystems worldwide (Walther et al. 2002, Parmesan and Yohe 2003, Isaak et al. 2012). Combined with additional stressors, such as habitat loss and invasive species, these changes are likely to shift patterns of distribution, abundance, phenology, and genetic diversity in many species. This is particularly true for many aquatic species restricted to stream environments with spatial gradients in temperature, flow, and physical habitat conditions. Understanding how changes in these environmental conditions influence patterns of demographic and genetic variation in stream networks is essential to designing effective conservation measures at both local and global scales.

Vulnerability assessments are a principal tool to understand the potential impacts of environmental change on populations, species, and ecosystems, and to inform conservation planning and management decisions (Cross et al. 2012). Such assessments allow us to explore the complex interactions caused by environmental change and their potential effects on local populations, improving our ability to identify vulnerable populations, species, and river reaches, and providing insight on the source of this vulnerability. Previously, the vulnerability of threatened and exploited stream species has been assessed based on either genetic or demographic factors alone (e.g., Fagan 2002, Jarić et al. 2010). Thus, there is an urgent need to develop novel modeling approaches to consider both demographic and genetic factors in understanding species responses to climate change.

We present a novel riverscape resistance modeling framework that combines the use of CDFISH with spatiotemporal changes in abiotic variables (e.g., dams, stream temperature, or flow regime) to assess and map the vulnerability of aquatic populations in a stream network. We focus the application on a large, complex, and connected river and lake network containing migratory salmonid (e.g., trout and char) populations that migrate throughout a freshwater river and lake network in northwestern Montana, USA, and southeastern British Columbia, Canada. Our first objective was to use the CDFISH-based framework to explore the behavior of genetic and demographic population vulnerability metrics in response to temperature and physical barrier-induced resistances to movement. This allowed us to assess effects of thermal suitability and connectivity of stream habitats on population vulnerability. Our

second objective was to develop and evaluate summary indices that combine demographic and genetic vulnerability metrics to assess the spatiotemporal change in overall vulnerability of populations. We considered four connectivity scenarios that illustrate the relative sensitivity of the six metrics and the combined vulnerability indices for detecting reduced connectivity (and population vulnerability), and for inferring the causes of vulnerability (e.g., partial vs. complete isolation). Finally, we applied this demogenetic framework to a bull trout metapopulation in the upper Flathead River system, Canada and USA, to help assess how current and predicted future stream warming may influence population viability. Our approach provides a general framework useful for population vulnerability assessments and strategic targeting of mitigation or restoration efforts in spatially complex aquatic systems experiencing multiple stressors.

Approach

We used a spatially explicit, individual-based, riverscape demogenetic program (CDFISH v0.52; Landguth et al. 2012) to assess how stream resistance and other features influence indices of population vulnerability in a hypothetical network of migratory trout populations. Our goal was to produce a genetic vulnerability index for each population to identify populations at risk under various riverscape scenarios (e.g., temperature or projected change in flows). Genetic vulnerability was defined as a combination of three metrics that estimate genetic diversity within populations, differentiation between populations, and temporal change in differentiation between populations. For each population j at every generation t we calculated the following metrics: (1) allelic diversity within a population, (2) mean of the pairwise genetic differentiation between a (focal) population and every other population, and (3) temporal change in population-specific pairwise genetic differentiation. The demographic vulnerability index was used to assess a population's risk of extirpation from demographic stochasticity resulting from small population size and low immigration. We characterized demographic vulnerability for each population based on three metrics, which provided estimates of the demographic status within populations, between populations, and over time (Fig. 2): (1) abundance (census size) within populations, (2) number of immigrants from other populations (strayers), and (3) change in abundance in populations

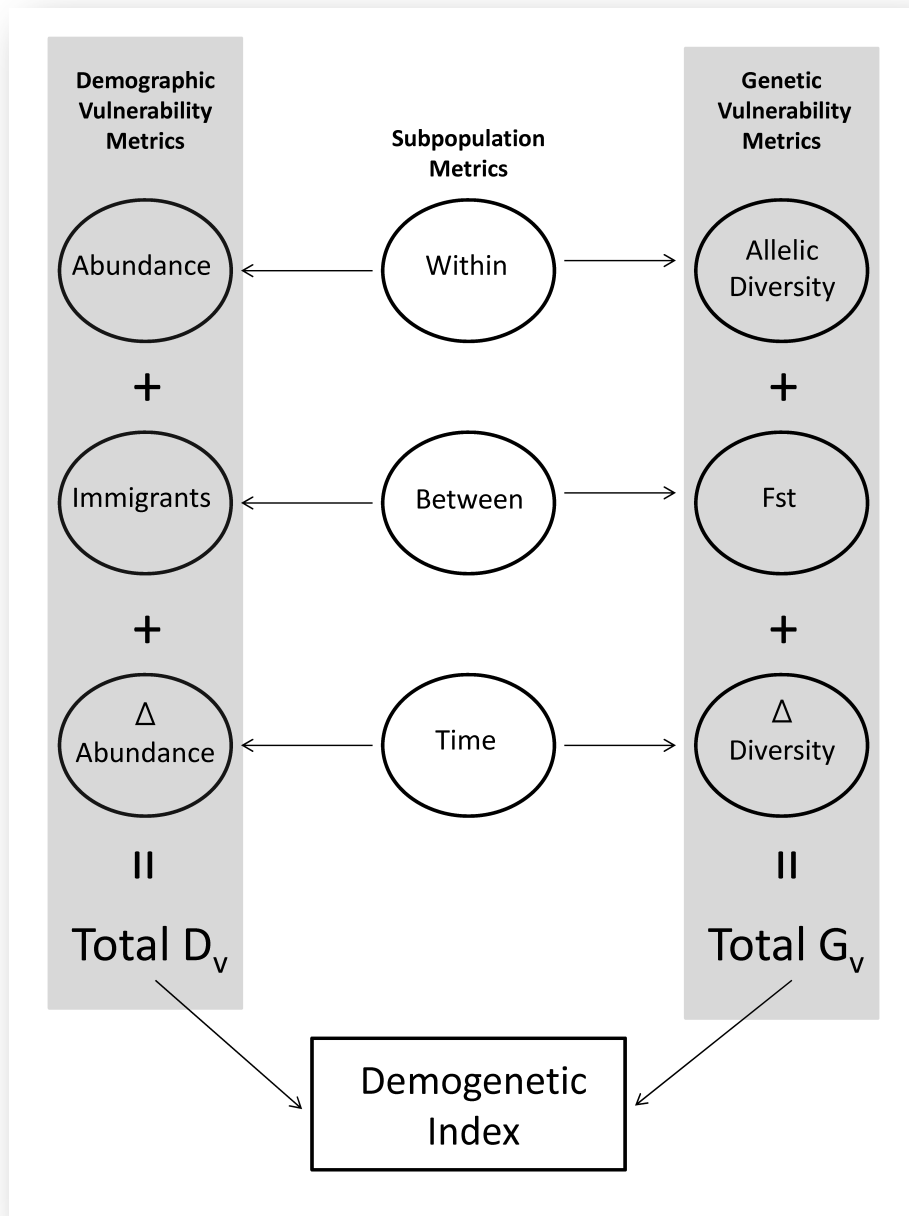


Fig 2. Demogenetic vulnerability flow diagram. The three genetic metrics (allelic diversity, differentiation [GST], and change in differentiation [DGST]) and the three demographic metrics (abundance, immigrants, and change [D] in abundance) that reflect within, between, and temporal population vulnerability (through demographic vulnerability [D_v] and genetic vulnerability [G_v]) are added together to produce demogenetic vulnerability indices (DGv).

We used the CDFISH program to assess how increasing stream resistance influenced indices of population vulnerability in a realistic network of migratory and resident bull trout populations. This empirical pilot study complements our hypothetical example by adding more realistic bull trout simulation parameters for temporal modeling to assess effects of future temperature increases on vulnerability, and by using more populations, which are initially parameterized using real demographic data (redd counts per population). We considered two scenarios: (1) a current stream temperature resistance to movement on which population dynamics were projected for the next 100 years, and (2) a projected future stream temperature resistance to movement on which population dynamics were projected for the next 100 years. See Landguth et al. (2014) for more details on the approach.

Results

Our hypothetical modeling scenarios illustrate the usefulness of a demogenetic resistance-modeling framework to identify populations vulnerable to environmental change and reduced connectivity within riverscapes. The hypothetical scenarios illustrated the differences in relative responses of demographic vs. genetic vulnerability in stream networks. Our hypothetical and empirically based modeling scenarios showed that warmer water temperatures and/or physical or hydrological barriers (e.g., low flows or dewatering) to movement (or the cumulative effect of distance traveled through these environments) are predicted to fragment suitable habitat for migratory salmonids, resulting in the potential loss of genetic diversity within populations and reduced population sizes. We show that different metrics have different relative sensitivities under four hypothetical (but realistic) resistance barrier scenarios for early detection of population isolation and vulnerability. Using empirical data in a pilot study on bull trout, we illustrate the usefulness of this approach for developing quantitative simulation-based predictions of climate change effects on connectivity and population vulnerability.

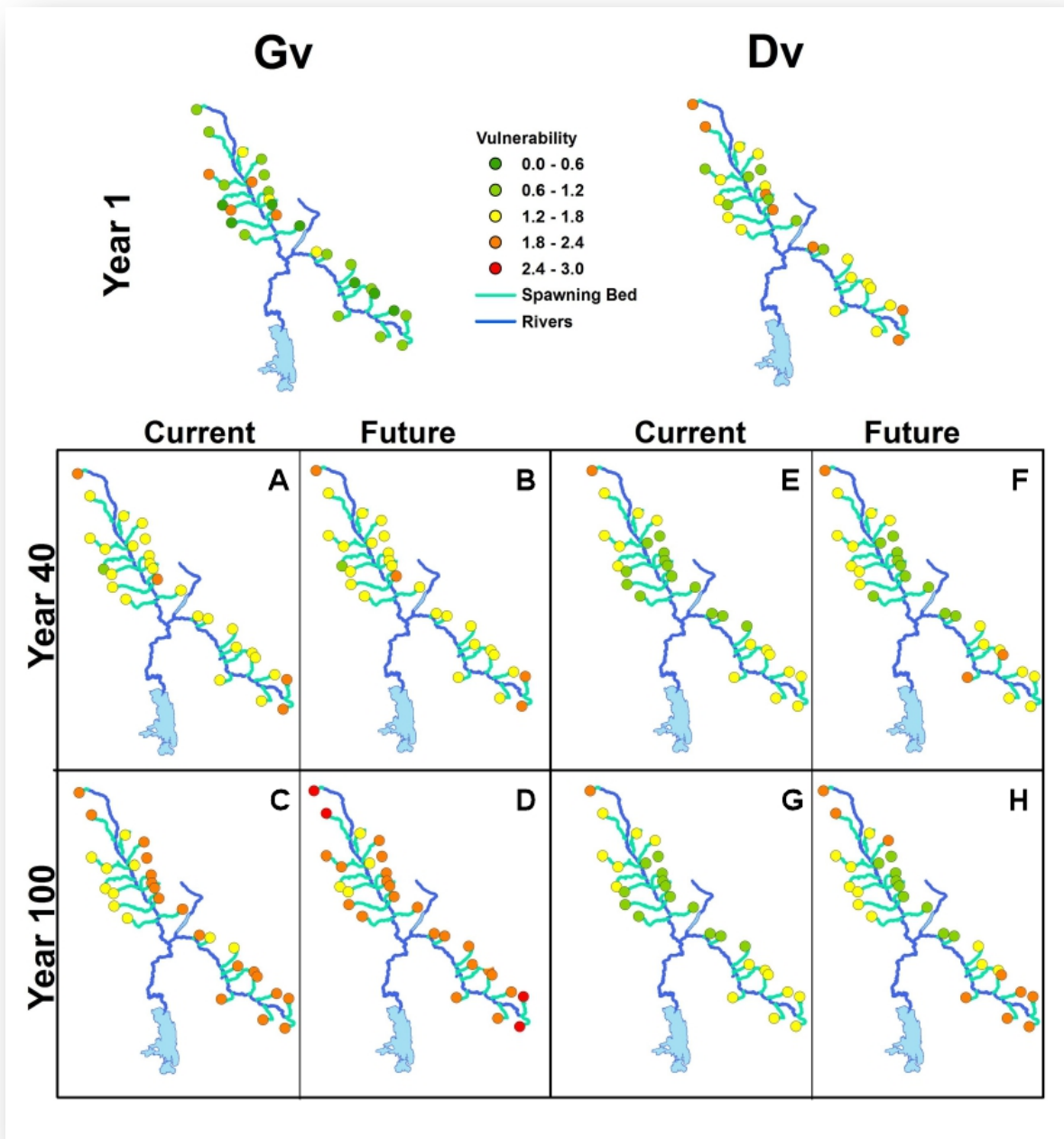


Fig. 3. Vulnerability heat maps for bull trout populations. Vulnerability indices for each of the 28 populations are represented by colors (red is the highest and green is the lowest) for Gv and Dv. Current temperature was used for years 0–40 and an example of vulnerability at year 1 is shown on the top row. At year 40, the modeled future temperature surface was inserted and the two scenarios are compared at this instance on the second row. The final year 100 of the simulations is plotted on the last row.

Conclusions

We introduce a novel simulation-modeling framework that uses riverscape resistance (i.e., connectivity) surfaces along with genetic and demographic information from individual-based simulations to assess the vulnerability of populations to environmental variation and anthropogenic impacts. This framework allows assessment of the contribution of individual genetic and demographic metrics (e.g., gene diversity and dispersal) to population vulnerability, and provides an overall demogenetic vulnerability index (combining all metrics) for each population within a stream network. The framework is flexible enough to include a range of alternative genetic and demographic metrics and to assess the interaction of environmental variables of interest for nearly any species or riverscape scenario. We show that different metrics have different relative sensitivities under four hypothetical (but realistic) resistance barrier scenarios for early detection of population isolation and vulnerability. Using empirical data in a pilot study on bull trout, we illustrate the usefulness of this approach for developing quantitative simulation-based predictions of climate change effects on connectivity and population vulnerability.

Management implications

Our demogenetic vulnerability-modeling framework can be used to identify conservation units that maximize genetic diversity, potential for local adaptation, and population abundance in freshwater systems. This framework can also be used to assess the potential impacts of climate warming (e.g., increased stream temperatures and decreased flows) on freshwater fishes and critical habitats, as we have demonstrated with the empirical analysis on bull trout populations. Our approach allows for fine-scale, spatially explicit vulnerability assessments at scales relevant to management needs (i.e., reach and stream scales), and moves beyond bioclimatic niche assessments by integrating additional measures affecting population persistence, genetics and demography, both of which are necessary to develop accurate and comprehensive vulnerability assessments for aquatic species. For example, results can be visualized using heat maps, which identify populations that are predicted to be the most vulnerable to harmful genetic and demographic changes caused by habitat fragmentation and population isolation (other maps available online). Such vulnerability maps can be used to identify isolated and combined genetic and/or demographic factors influencing population persistence, and to evaluate the interactions between environmental change and demogenetic characteristics (e.g., gene flow, dispersal, migration). Our demogenetic vulnerability modeling framework can be used to understand connectivity and genetic diversity of populations across diverse habitats to restore, maintain, and monitor adaptive potential of

aquatic species. We hope this vulnerability modeling framework stimulates additional modeling developments and applications to help identify populations vulnerable to environmental change, and to improve conservation and management of freshwater populations, species, and ecosystems.

Objective 3: Assess how climatic variation and vulnerability is related to genetic diversity of threatened bull trout throughout the PNW

Ryan P. Kovach, Clint C. Muhlfeld, Alisa A. Wade, Brian K. Hand, Diane C. Whited, Patrick W. DeHaan, Robert Al-Chokhachy, Gordon Luikart. *In press*. **Genetic diversity is related to climatic variation and vulnerability in threatened bull trout.** *Global Change Biology*.

Summary

*Understanding how climatic variation influences ecological and evolutionary processes is crucial for informed conservation decision-making. Nevertheless, few studies have measured how climatic variation influences genetic diversity within populations or how genetic diversity is distributed across space relative to future climatic stress. We tested whether patterns of genetic diversity (allelic richness) were related to climatic variation and habitat features in 130 bull trout (*Salvelinus confluentus*) populations from 24 watersheds across the Columbia River Basin, USA. We then determined whether bull trout genetic diversity was related to climate vulnerability at the watershed scale, which we quantified on the basis of exposure to future climatic conditions (projected scenarios for the 2040s) and existing habitat complexity. We found a strong gradient in genetic diversity in bull trout populations across the Columbia River Basin, where populations located in the most upstream headwater areas had the greatest genetic diversity. After accounting for spatial patterns with linear-mixed models, allelic richness in bull trout populations was positively related to habitat patch size and complexity, and negatively related to maximum summer temperature and the frequency of winter flooding. These relationships strongly suggest that climatic variation influences evolutionary processes in this threatened species, and that genetic diversity will likely decrease due to future climate change. Vulnerability at a watershed scale was negatively correlated with average genetic diversity ($r = -0.77$; $P < 0.001$); watersheds containing populations with lower average genetic diversity generally had the lowest habitat complexity, warmest stream temperatures, and greatest frequency of winter flooding. Together, these findings have important conservation implications for bull trout and other imperiled species. Genetic*

diversity is already depressed where climatic vulnerability is highest; it will likely erode further in the very places where diversity may be most needed for future persistence.

Purpose and Objectives

In this study, we address two major objectives: (1) quantify how climatic and physical habitat variation are related to bull trout genetic diversity within local populations; and (2) measure the degree to which genetic diversity among watersheds covaries with metrics of bull trout exposure and sensitivity to climate change. To address the first objective, we used genetic data from 130 bull trout populations across the Columbia River Basin, USA, including 24 watersheds (i.e., ~4th to 7th order river sub-basins) nested within four conservation recovery units to quantify relationships between population genetic diversity and habitat and climatic factors. This information provides insight into long-term (average effective population size (drift) and connectivity (gene-flow) over time) and recent processes (population bottlenecks) influencing demography. Based on bull trout ecology, we hypothesized that genetic variation would be negatively associated with climatic stressors (e.g., high summer temperatures, winter flooding) and positively associated with habitat patch size and complexity.

To address the second objective, we evaluated bull trout vulnerability at a watershed-level based on exposure to forecasted climatic conditions and sensitivity to those forecasts, on the basis of current habitat complexity, but excluded adaptive capacity. We then compared vulnerability estimates to average genetic diversity among populations within a watershed. If vulnerable populations or groups of populations (metapopulations within a watershed) have relatively high genetic diversity, there may be adaptive potential in the face of rapid environmental change and low contemporary risk of negative inbreeding effects. Conversely, the opposite relationship would indicate that populations or metapopulations most susceptible to climate change are at additional risk from low genetic diversity, both in terms of evolutionary resiliency and reduced fitness owing to reductions in genomic variation. Overall, the results from this study provide a needed example of how genetic diversity can be used to describe the impacts of climatic variation on evolutionary processes and inform inferences about species' resilience to climatic and habitat changes at large spatial scales.

Approach

We used genetic data from 6,086 bull trout individuals spanning 130 populations and a sample size corrected estimate of allelic richness (here forward allelic richness = AR) to describe within-population genetic diversity. We hypothesized that genetic diversity in bull trout populations would be

positively associated with habitat patch size, habitat complexity, and summer base flow, and negatively associated with summer temperature, and winter flooding occurrence. Various predictor variables were used to describe these general hypotheses. We used standard linear and linear mixed effects modeling to identify variables related to bull trout genetic diversity and quantify relationships.

We assessed bull trout vulnerability to climate change at the watershed-scale by using future stream temperature and flow projections as metrics of *exposure*, and existing proportion of valley bottom habitat (habitat complexity) as a proxy metric for *sensitivity* to climate exposure. We compared vulnerability (exclusive of adaptive capacity) to observed patterns of genetic diversity to assess the degree to which they were correlated across space. If genetic diversity is negatively related to exposure and sensitivity, bull trout may have reduced adaptive capacity and increased risk of inbreeding depression in the face of environmental change.

We focused our efforts at the watershed scale (as opposed to local populations) because it is congruous with current conservation designations for bull trout core areas and climatic projections were available at this scale for the entire Columbia River Basin. To quantify exposure metrics, we used future projections of maximum summer stream temperature and frequency of high winter flows events (number of days exceeding the 95th percentile of annual flows) at the mouth of each watershed for which we had genetic data. Bull trout sensitivity to climate conditions was approximated on the basis of habitat complexity, estimated as the proportion of unconfined valley bottom relative to the total spawning and rearing habitat in each watershed. To summarize vulnerability, we added re-scaled exposure and sensitivity metrics (maximum stream temperature + winter flood risk + habitat complexity) for each watershed to obtain an overall vulnerability value. We then calculated correlations between vulnerability values and observed genetic diversity across watersheds.

Results

Allelic richness (AR) within bull trout populations across the Columbia River generally increased from west to east (hence the need for mixed models that accounted for spatial autocorrelation in bull trout genetic diversity). Specifically, AR was lowest in the Coastal recovery unit, moderate in both the mid-Columbia and upper-Snake, and highest in the upper-Columbia. We found evidence that habitat complexity (positive), stream length (positive), winter-flood frequency (negative) and maximum summer temperature (negative) were related to bull trout AR within local populations across the Columbia River Basin (Fig. 4). Overall, habitat complexity appeared to best-predict bull trout AR. Within climatic

variables there was some evidence that maximum summer temperature better predicted AR than winter flood frequency.

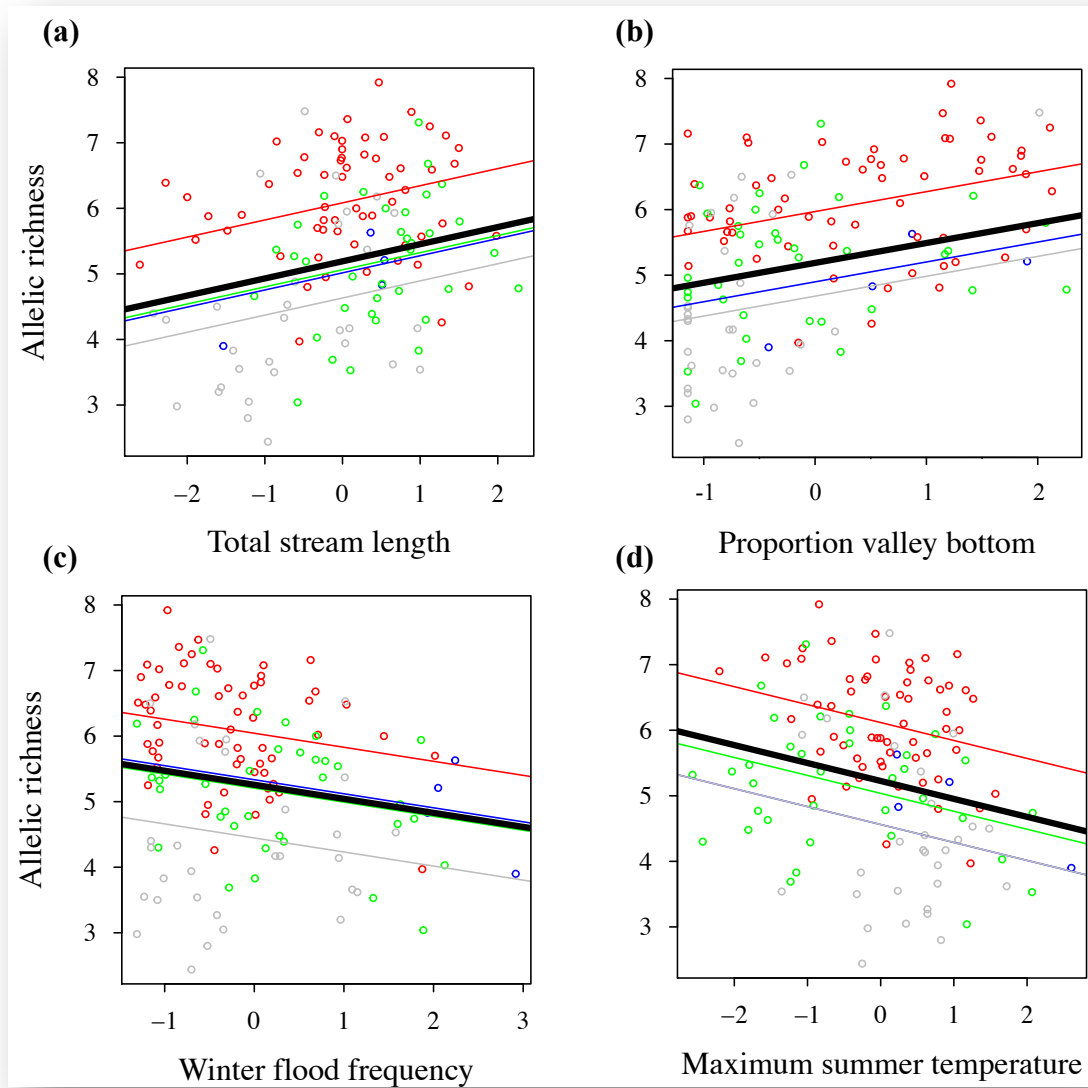


Fig. 4. Relationships between bull trout allelic richness and total stream length **(a)**, proportion valley bottom habitat **(b)**, winter flood frequency **(c)**, and maximum summer temperature **(d)** in critical spawning and rearing habitats. Values for predictor values are standardized. The solid black line is the overall mean population response, while the colored lines and circles represent the four recovery units: Coastal (blue), mid-Columbia (green), upper-Snake (grey), and upper-Columbia (red).

Maximum summer temperature and winter flood frequency were predicted to increase in nearly every watershed (23 of 24 for temperature and 24 of 24 for flooding) from present to the 2040s (Fig. 5). On average, watersheds were predicted to be 1.15 °C (SD = 0.57) warmer and have 2.80 (SD = 2.01) more winter flood days per year compared to current conditions. Relative to current conditions, the predicted shift in flow is much greater and represents an increase of 82%, while the change in temperature is only a 5% increase. Projected maximum summer stream temperatures and winter flood risk (i.e., climatic exposure) generally increased from east to west and north to south for watersheds where multiple spawning populations of bull trout were sampled. Proportion of valley bottom habitat (i.e., inversely related to sensitivity) and average AR generally had the opposite pattern.

Climatic vulnerability at the watershed-level was highest in the southwest portion (e.g., John Day and Malheur watersheds) and lowest in the headwaters (e.g., Flathead and Swan watersheds) of the Columbia River Basin. The correlation (r) between average AR and vulnerability was -0.767 ($P < 0.001$). Thus, projected vulnerability was highest in those watersheds where genetic diversity was lowest (Fig. 5).

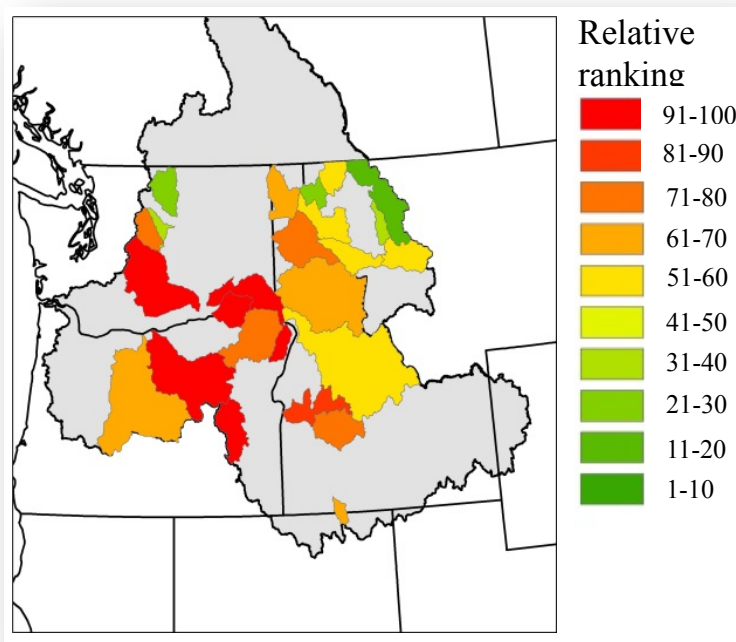


Fig. 5. Projected (2040s) climatic vulnerability of bull trout at the watershed scale across the Columbia River Basin. Higher values represent higher vulnerability to future climate change.

Conclusions

Although genetic diversity is critical for long-term viability, especially in rapidly changing environments, our understanding of how climatic variation is related to population genetic diversity and the implications of such relationships for species' susceptibility to climate change is limited. We showed that genetic diversity at large spatial scales is associated with climatic drivers likely to shift substantially over the next century. Specifically, genetic diversity in bull trout populations throughout the Columbia River Basin was positively related to habitat patch size and complexity, and negatively related to maximum summer temperatures and frequency of winter flood events. These physical habitat and climatic variables are similarly related to bull trout occupancy, survival, and habitat selection, indicating that demographic risk for this species may be positively associated with evolutionary risk from climate change.

We also found that genetic diversity of bull trout populations was generally lowest in portions of the Columbia River Basin where we estimated future vulnerability (exposure + sensitivity) to climate change was highest. This pattern may be consistent for other vertebrate species threatened by climate warming, especially ectothermic organisms whose population dynamics are strongly influenced by climatic conditions. Additional studies focused on identifying relationships between genetic diversity and climatic variability across large spatial scales could help determine the ubiquity of this pattern, and enhance conservation decision-making by identifying those areas of a species range where populations are threatened demographically and/or evolutionarily.

Management implications

For conservation and management, relationships between genetic diversity and climatic variation can be used to augment other sources of information (e.g., bioclimatic envelope models, physiological tolerances, etc.) to better understand current threats to population persistence and potential vulnerability to climatic change. At present, a major source of uncertainty is how neutral or adaptive genetic diversity influence adaptive potential on ecological time scales. However, microevolution in response to climate change can occur rapidly in salmonid fishes, highlighting that genetic diversity can offer resiliency in the face of climatic change. Nevertheless, genetic diversity remains neglected in conservation and management decision-making worldwide, especially in the context of climate change. To address this deficiency, additional efforts are needed to describe how genetic diversity is distributed across the landscape relative to climatic and habitat variation so that we

can ultimately understand and predict the ecological and evolutionary consequences of climatic change for global biodiversity.

Objective 4: Assess how climate and habitat characteristics influence genetic diversity of steelhead across the PNW

Hand, Brian K., Ryan P. Kovach, Clint C. Muhlfeld, Alisa A. Wade, Diane C. Whited, Shawn R. Narum, Andrew P. Matala, John S. Kimball, Jack S. Stanford, Gordon Luikart. **Climate Variables Explain Genetic Differentiation within Metapopulations: The Importance of Replication and Uncertainty Assessments in Landscape Genetics.** Molecular Ecology. In Revision.

Summary

*Understanding how environmental variation influences population genetic structure is increasingly important for conservation management because it can reveal how human-induced global change impacts population connectivity, genetic diversity and persistence. We used riverscape genetics modeling to assess whether climatic and habitat variables were related to genetic differentiation (F_{ST}) within each of five metapopulations (79 populations) of threatened steelhead trout (*Oncorhynchus mykiss*) in the Columbia River Basin, USA. We found that F_{ST} was positively correlated with winter precipitation ($r = 0.63-0.75$) and negatively correlated with summer maximum temperature ($|r| = 0.53-0.76$) within three metapopulations (Salmon, Eastern Cascades and John Day), while the proportion of habitat patch size was positively correlated with F_{ST} ($r = -0.81$) in the Lower Columbia metapopulation. We also applied a more stringent Bayesian approach to relating climatic and habitat variables to F_{ST} and found support for winter precipitation in two metapopulations (Salmon and Eastern Cascades) and summer maximum air temperature in one metapopulation (John Day). Finally, sensitivity analysis revealed little change in riverscape genetic relationships in four of the five metapopulations, suggesting results are robust to data availability. By using both replication (multiple metapopulations) and sensitivity analysis, we were able to identify consistent relationships between climate and F_{ST} in several metapopulations, while highlighting key areas of uncertainty across the entire drainage. Taken together, our findings provide empirical evidence that riverscape and climatic variables may shape the genetic structure of steelhead populations while highlighting the need for caution when extrapolating results from one study area to another.*

Purpose and Objectives

Many wild salmonid populations and species have declined dramatically over the past century primarily due to overharvest, negative interactions with cultured stocks, and freshwater habitat degradation and loss. Climate change will have direct consequences for many salmonid fishes because their population dynamics can be directly impacted by variation in stream temperature and flow (Jonsson and Jonsson 2009) both of which are predicted to change dramatically in coming decades (Mantua et al 2010). Additionally, climate change will likely exacerbate existing stressors of habitat fragmentation and degradation on salmonid population connectivity in fresh water (Parmesan 2006), especially for anadromous salmonids that have strong spawning fidelity for natal streams that are located hundreds to thousands of kilometers upstream from the ocean.

To identify contemporary factors important to future climate change we tested whether climatic and habitat variables were currently associated with genetic differentiation (population specific F_{ST}) within five steelhead (*Oncorhynchus mykiss*; the anadromous form of rainbow trout) metapopulations (79 total populations; Fig. 4) segregated within the Columbia River Basin. First, we identified a range of hypotheses of how climate and habitat variables may influence genetic differentiation within metapopulations and identified eight proxy measures to represent each (including winter precipitation, winter highest 5% flows, summer maximum temperature, summer mean flow, critical habitat length, critical habitat proportion, length of unconfined valley bottom and stream distance). Next, we assessed correlations within metapopulations using estimates of environmental variables for each local population and population specific F_{ST} values. We also used a hierarchical Bayesian model (GESTE; Foll & Gaggiotti 2006) to identify which of our selected environmental variables most influenced population specific F_{ST} values in each of the five metapopulations. Finally, we used model sensitivity analyses to test the consistency of our predicted correlations within each metapopulation to allow for more robust inference than most studies in riverscape genetics, which often lack replication and sensitivity assessments.

Approach

We used genetic data from 79 wild populations of steelhead representing five metapopulations within the Columbia River Basin, USA (Fig. 6). We used genotypic data spanning the years of 1996–2011 from 4583 adult and juvenile steelhead trout with 180 loci. We hypothesized that the genetic structure within steelhead metapopulations would be correlated with stream temperature and flow (climate

variables), and a suite of physical variables that quantify habitat for steelhead spawners and juveniles (winter precipitation, winter highest 5% flows, summer maximum temperature, summer mean flow, critical habitat length, critical habitat proportion, length of unconfined valley bottom and stream distance).

We used GESTE (GEnetic STRucture inference based on genetic and Environmental data), a hierarchical Bayesian model, to determine the best combinations of climatic and habitat characteristics influencing patterns of genetic differentiation within metapopulations. The GESTE program works by calculating population specific values of F_{ST} for all populations from allele frequency data and uses a general linear model (GLM) to estimate the relationship(s) between an environmental variable(s) and F_{ST} values.

Sensitivity analysis was used to further provide confidence in the selection of environmental variables that were significantly correlated when using all populations within a metapopulation. Therefore, we iteratively removed data for a single population (i.e. jackknifing) and then recalculated Pearson correlation (r) values for the remaining populations within a metapopulation. Changes in the most highly correlated environmental variables were considered important to conservation management because of the potential change in the hypothesis associated with a different environmental variable. For example, a switch from winter precipitation to critical habitat length would indicate a different relationship between environment and genetic diversity (F_{ST}).

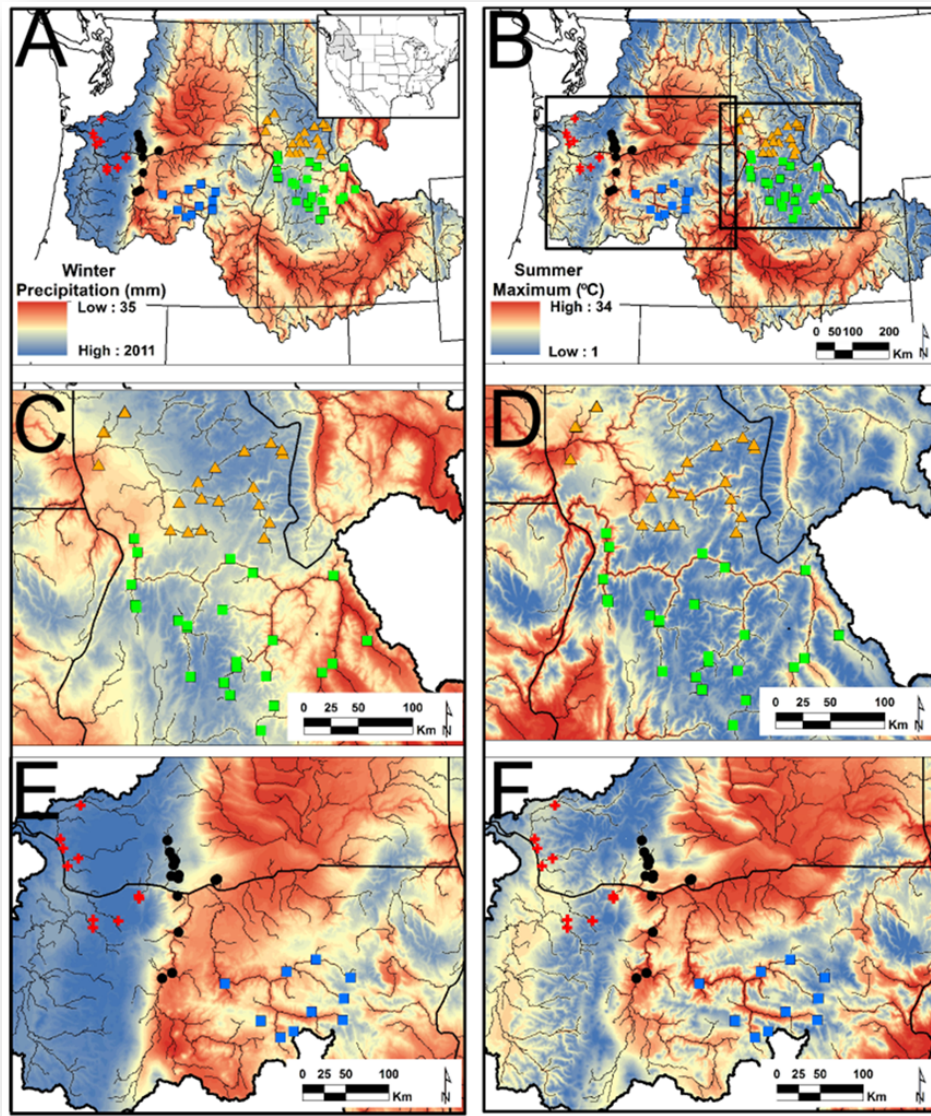


Fig. 6. Map of the five metapopulations (study areas) of steelhead relative to summer maximum temperature and winter precipitation. The top panels depict summer maximum temperature (A) and winter precipitation (B) at the full extent of the Columbia River Basin, USA. Panels (C) and (E) are blowups of the areas delineated in panel (B) with winter precipitation as a background. Panels (D) and (F) are blowups of the same areas with summer maximum temperature as the background. Points represent local populations of steelhead, colored by their corresponding metapopulation (red crosses = Lower Columbia, black circles = Eastern Cascades, blue squares = John Day, orange triangles = Clearwater, green squares = Salmon). 0

Results

We found that winter precipitation was positively correlated with F_{ST} in three of five steelhead metapopulations (Salmon: $r = 0.68$, $P < 0.01$, Eastern Cascades: $r = 0.75$, $P < 0.01$; John Day: $r = 0.63$, $P = 0.05$; Fig. 7). In the same three metapopulations, we found a negative correlation with F_{ST} and summer maximum temperature (Salmon: $r = -0.53$, $P < 0.01$; Eastern Cascades: $r = -0.76$, $P < 0.01$; John Day: $r = -0.65$, $P = 0.04$; Fig. 7). Additionally, we found significant correlations between F_{ST} and summer mean flow ($r = -0.76$, $P < 0.01$) in the Eastern Cascades, and between F_{ST} and critical habitat proportion ($r = -0.81$, $P < 0.01$) in the Lower Columbia. We found no significant correlations between environmental variables and F_{ST} in the Clearwater; for which stream distance was the most highly correlated variable ($r = 0.35$, $P = 0.11$).

Winter precipitation was well supported in the GESTE model in two of five metapopulations including in the Salmon (Pr = 0.68; where Pr is the probability of a model being selected as the top model in runs of GESTE) and the Eastern Cascades (Pr = 1.0). Genetic differentiation was positively related to winter precipitation (i.e. differentiation was highest in those populations where winter precipitation was highest) in both the Salmon ($b = 0.50$; 95% HPDI = 0.21–0.77) and Eastern Cascade ($b = 0.69$; 95% HPDI = 0.27–1.13) metapopulations. The 95% HPDI refer to the 95% highest probability density interval around each parameter estimate.

We found additional support for climatic and habitat variables in Eastern Cascades, John Day and Lower Columbia. In the Eastern Cascades, summer mean flow had substantial support (Pr = 1.0; $b = -0.70$; 95% HPDI = -0.29–1.13). In the John Day, summer maximum temperature, which was negatively related to F_{ST} ($b = -0.51$; 95% HPDI = -0.09–0.97), had the highest individual support (Pr = 0.54). In the Lower Columbia, critical habitat proportion was negatively related to F_{ST} ($b = -0.43$; 95% HPDI = -0.12–0.76) and had the greatest support (Pr = 0.62) among models explaining differentiation within this metapopulation. For the Clearwater, we found no support for any environmental variables; the null model (where only the constant intercept-only term is included) had the greatest support (Pr = 0.78).

Results from the sensitivity analyses revealed mixed uncertainty in model selection results among replicate metapopulations. In the Salmon metapopulation, where we found a strong relationship between F_{ST} and winter precipitation, we found no change in this relationship when we iteratively removed each population. In the John Day, Lower Columbia and Eastern Cascades we observed changes in the strength of correlation between environmental variables and F_{ST} . In the John Day, these changes had potential management implications (described below), but were of less concern in the Lower Columbia and Eastern Cascades.

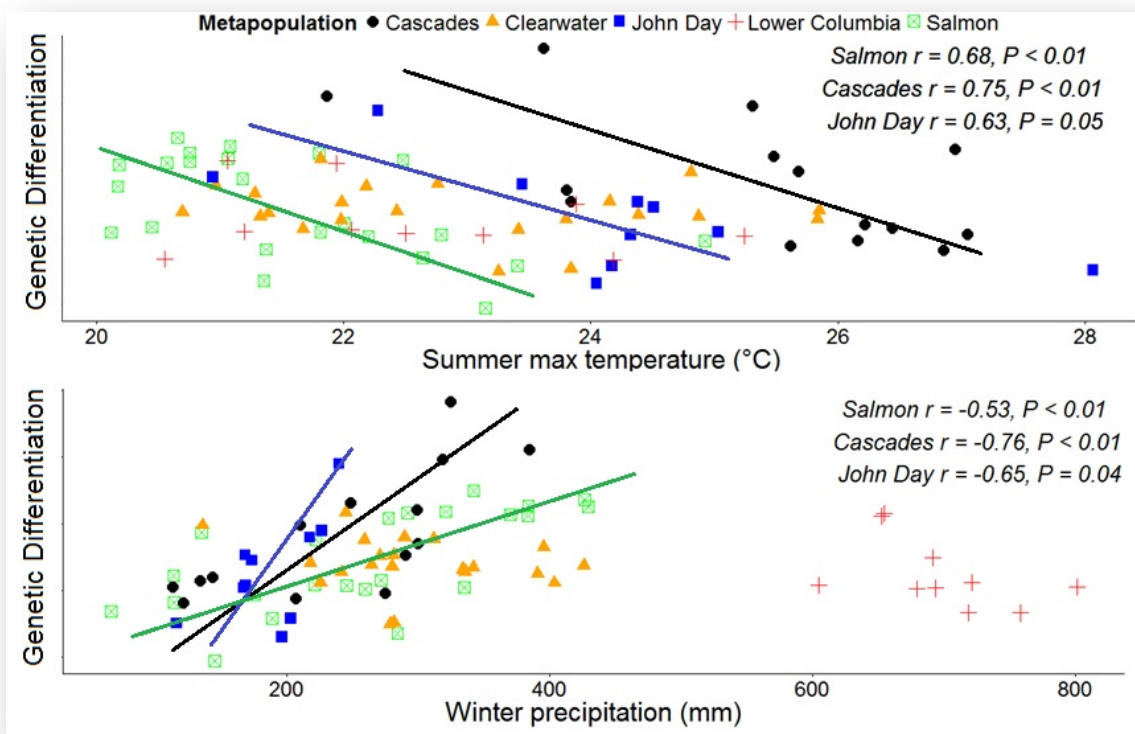


Fig. 7. Scatter plots of measurements for each population for summer maximum temperature and winter precipitation. Points represent local populations of steelhead, colored by their corresponding metapopulation (red crosses = Lower Columbia, black circles = Eastern Cascades, blue squares = John Day, orange triangles = Clearwater, green squares = Salmon). The y-axis values on the right panel are genetic differentiation (the natural log transform values of F_{ST} used in GESTE) on which environmental variables are fitted using linear regression.

Conclusions

We found significant correlations between climatic variables—winter precipitation and summer maximum temperature—and genetic differentiation (F_{ST}) in several metapopulations (Eastern Cascades and the John Day) of steelhead trout. Bayesian models provided further support that winter precipitation (but not summer maximum temperature) is related to genetic differentiation in the Salmon and Eastern Cascades metapopulations. Thus, precipitation—a surrogate for stream flow hydrology—appears to play an important role in driving patterns of genetic variation in several major watersheds of the Columbia River Basin.

Winter precipitation falling primarily as snow results in increased winter snowpack and increased peak spring runoff, thereby potentially increasing streambed scour of steelhead redds during embryo incubation periods (late February–June; Goode *et al.* 2013; Matala *et al.* 2014). This could cause high embryo mortality resulting in reduced local effective population sizes (N_e), thereby causing increased genetic drift within populations and *higher* F_{ST} values between populations. Indeed, the three metapopulations areas with greatest correlations between winter precipitation and F_{ST} (Salmon, Eastern Cascades, and John Day) are predominately snow-dominant basins with peak flows during the spring (Hamlet *et al.* 2013) when steelhead embryos are incubating. Similarly, major differences in stream flow or thermal regime often generate strong, genetically based (i.e. locally adaptive) differences in reproductive timing across populations (e.g. Taylor 1991). Reproductive isolation owing to local adaptation to heterogeneous climatic variation can drive strong genomic differentiation, a pattern that is commonplace in salmonid fishes (Hendry and Day 2005). Together, redd scouring itself, and local adaptation in reproductive timing to avoid scouring, could interact to generate the observed patterns in steelhead genetic differentiation.

The observed negative correlation between temperature and genetic diversity observed in the Salmon, Eastern Cascades and John Day were contrary to our original hypothesis; we expected that elevated temperatures may increase mortality and thus increase drift and differentiation. In cold, high-latitudes regions, increased temperatures can increase growth and survival rates (Richter and Kolmes 2005). However, the average summer maximum air temperature in the Eastern Cascades (25°C) and the John Day (24°C) are likely limiting overall to juvenile growth and survival (Richter and Kolmes 2005). Thus, a more plausible explanation in these metapopulations may be that migration (gene flow) routes with stream temperatures over 21–22°C are potentially limited by temperature (Richter and Kolmes 2005). In the second scenario, temperature may play a role in facilitating straying when migration to natal streams are blocked or limited, leading to lower F_{ST} (Bradford *et al.* 2009).

Sensitivity analysis indicated that results for the John Day (with only 10 populations) were potentially dependent on the data used during analysis and that removing a single population changed model selection results. This change in results is important because it indicates that conservation management could follow alternative strategies depending on data availability. For example, the first result might indicate that future management focus on monitoring changes in climate (e.g. temperature) while the second result, instead, may indicate habitat quality is more important. In the second case, more active mitigation might be possible towards actively improving the quality and size of available habitat while the first case may present few opportunities for mitigation.

For the Lower Columbia and Eastern Cascades, we also observed changes to model selection results across jackknife replicates, where secondary or less significant variables (winter highest 5% flows in the Eastern Cascades and critical habitat in the Lower Columbia) gained support depending on the data used during analyses. Unlike the John Day, we concluded the observed changes did not signal a major change to the underlying hypotheses (i.e. streambed scouring in the Eastern Cascades and increased stream carrying capacity in the Lower Columbia). For example, the winter highest 5% flows and winter precipitation (in the Eastern Cascades) were originally identified as proxy measures of the same hypothesis. Likewise in the Lower Columbia, critical habitat and proportion of critical habitat are also very similarly related to the amount of available habitat.

Management Implications

The surprisingly high correlations we found between climatic variables (precipitation and summer maximum temperature) and genetic differentiation (population specific F_{ST}) in three metapopulations suggest that future studies should further explore the potential influence of climate change on population connectivity in salmonids. This information will further aid conservation when assessing future salmonid population vulnerability and viability. As important for conservation management, future investigations should consider additional variables (e.g. habitat degradation, pollution, hatcheries and life-history variation) that may be influencing genetic differentiation, specifically in the Clearwater where we observed no significant relationships between climate and habitat with genetic diversity. Replication of study areas (metapopulations) was key in illuminating important differences in the Clearwater compared to other metapopulations. Generally, replication in riverscape (and landscape) genetic studies is seldom conducted, but is critical for improving general understanding of population connectivity and furthering our confidence in subsequent management decisions. Within replicate metapopulations, sensitivity analyses can help assess the overall robustness of riverscape connectivity model selection and provide understanding of model uncertainty. Our model sensitivity analysis showed support for similar hypotheses in four, but not all five, metapopulations. Overall, we recommend better quantification of model uncertainty and using replicate metapopulations when possible in all riverscape (and landscape) genetic studies. The inclusion of uncertainty and model reliability assessments will improve general understanding and forecasting of patterns of genetic variability within and among study areas, and further landscape genetics as a predictive discipline for connectivity modeling, management and biodiversity conservation.

Objective 5: Assess the vulnerability of steelhead and bull trout to climate change effects across the PNW

Wade, Alisa A., Brian K. Hand, Diane C. Whited, Ryan P. Kovach, Gordon Luikart, Clint C. Muhlfeld. In-prep. **Steelhead trout and bull trout vulnerability to climate change: a multi-species assessment for the Columbia River Basin.**

Summary

*Natural resource managers are increasingly using climate change vulnerability assessments (CCVAs) to plan for and mitigate potential impacts of future climate change on species, populations and ecosystems. Salmonids are one of many species at risk due to their previous adaptation to cold water and specific hydrological regimes that influence spawn timing and migration among other life history traits. Therefore, salmonids are likely to experience large shifts in both temperature and flow regime under future changes in climate. Though CCVAs are a vital tool in understanding the potential impacts of climate change, most previous CCVAs fail to include genetic and demographic components critical to species viability. Here we take a multispecies approach to CCVAs by assessing potential climate threats to two salmonid species with different life histories - steelhead trout (*Oncorhynchus mykiss*) and bull trout (*Salvelinus confluentus*). We completed a novel assessment of climate vulnerability for 47 bull trout and 46 steelhead metapopulations throughout the Columbia River Basin. When including both genetic and demographic data into our model we found there to be a large range of vulnerability ratings predicted by the CCVA that can occur depending on the data included in the final model. For example, in steelhead, the addition of a genetic component showed an overall trend of increasing vulnerability while the inclusion of demographic data lowered vulnerability rating. Although our approach is applied to two species of salmonids, we illustrate the importance of including demographic and genetic factors, in addition to climatic and habitat when conducting a CCVA.*

Purpose and Objectives

Increasingly, resource managers and conservation scientists are urgently working to proactively and effectively plan for potential climatic changes. In response, there has been a dramatic increase in the use of climate change vulnerability assessments (CCVAs) to identify systems, species, and populations at risk (Glick et al 2011). CCVAs are important to salmonid conservation because they provide a framework to understand how environmental stressors impact species persistence so as to

ascertain potential for conservation intervention. Per Intergovernmental Panel on Climate Change (IPCC) definitions, CCVAs should account for the three elements of vulnerability: 1) exposure (magnitude or risk of physical changes in climate conditions), 2) sensitivity (likelihood of adverse effects to a system given climate changes; akin to dose-response) and 3) adaptive capacity (intrinsic ability for a system to reduce its sensitivity by successful response to changing climate) (IPCC 2007). To reflect the IPCC definition of vulnerability and gain ecologically relevant insight into the mechanisms linking climatic change to variation in salmonid genetic diversity, robust CCVAs need to account for demographic *and* genetic indicators of salmonid population status.

Here, we applied a more holistic approach to CCVAs by using multiple species and taking a more explicit approach to integrating climate exposure and habitat measures with demographic and genetic metrics. We choose two salmonid species with very different life history traits (anadromous steelhead vs. non-anadromous bull trout) that exist sympatrically and non-sympatrically throughout the Columbia River Basin (CRB). In addition to testing two future scenarios of climate change, we conducted sensitivity analysis. Sensitivity analysis consisted of calculating vulnerability ratings using the full complement of metrics (exposure, habitat, demographic and genetic), along with “simple” models including exposure combined with one additional metric. Overall, our results provide managers with a more thorough understanding of salmonid vulnerability throughout the CRB. Further, we hope to alert managers to data-dependent idiosyncrasies that typically might be overlooked when not taking into account more sources of data or when not conducting sensitivity analysis.

Approach

We collected environmental, demographic and genetic data for 47 bull trout and 46 steelhead metapopulations. For each steelhead and bull trout metapopulation, we calculated proxies to represent the three primary vulnerability elements (exposure, sensitivity, adaptive capacity) which we further divided into four sub-elements including: climate, habitat, demographic and genetic (Fig. 8). For both steelhead and bull trout these metrics included: two climate metrics based on NASA NEX-DCP30 climate models (proportional increase in stream areas exceeding key thermal thresholds and projected increase in runoff), three habitat metrics derived from satellite products (floodplain and critical habitat length and index of human modification), a demographic (estimated abundance) and a genetic (allelic richness) metric. For bull trout, we used three additional metrics accounting for differences in life history (resident vs. migratory), the number of populations present in a metapopulation, and the estimated

impact of invasive species (e.g., lake trout, brook trout, brown trout, etc.). For steelhead we considered winter and summer run separately in analysis.

To calculate our vulnerability ratings we first rescaled all metrics 1-100 (100 = “highest vulnerability”). We then took the average of all metrics under each element, for example the average of the two climate metrics to represent exposure (E) and the average of the three habitat metrics to represent habitat (H). Then we calculated an overall vulnerability = $E + H + D + G$, where D was the demographic metric and G was the genetic metric. Finally, we qualitatively compared the change in vulnerability value when only considering the following subset of elements: 1) E + H, 2) E + H + G, 3) E + D.

Results

For the full bull trout model (E + H + D + G), vulnerability ratings showed a higher proportion of relative vulnerability for metapopulations in the south vs. the north. The John Day River showed the highest relative vulnerability while metapopulations in the Flathead River drainages showed lower relative vulnerability. However, most major drainages appeared to have at least one metapopulation at higher relative risk. The average difference in vulnerability ratings (avg = 4.16, SD = 8.2) between the simple habitat model (E + H) and the simple demographic model (E + D) was nearly equal to the average difference (avg = 4.91, SD = 11.6) between the simple habitat model and the simple genetics model (E + G). Overall, there was little average difference, but high variation (avg = 0.75, SD = 12.2) between vulnerability ratings calculated using the simple demographics model and the simple genetics model. However, sensitivity analysis did not appear to reveal any single metric (genetic, demographic or habitat) was highly influential in determining final metapopulation vulnerability.

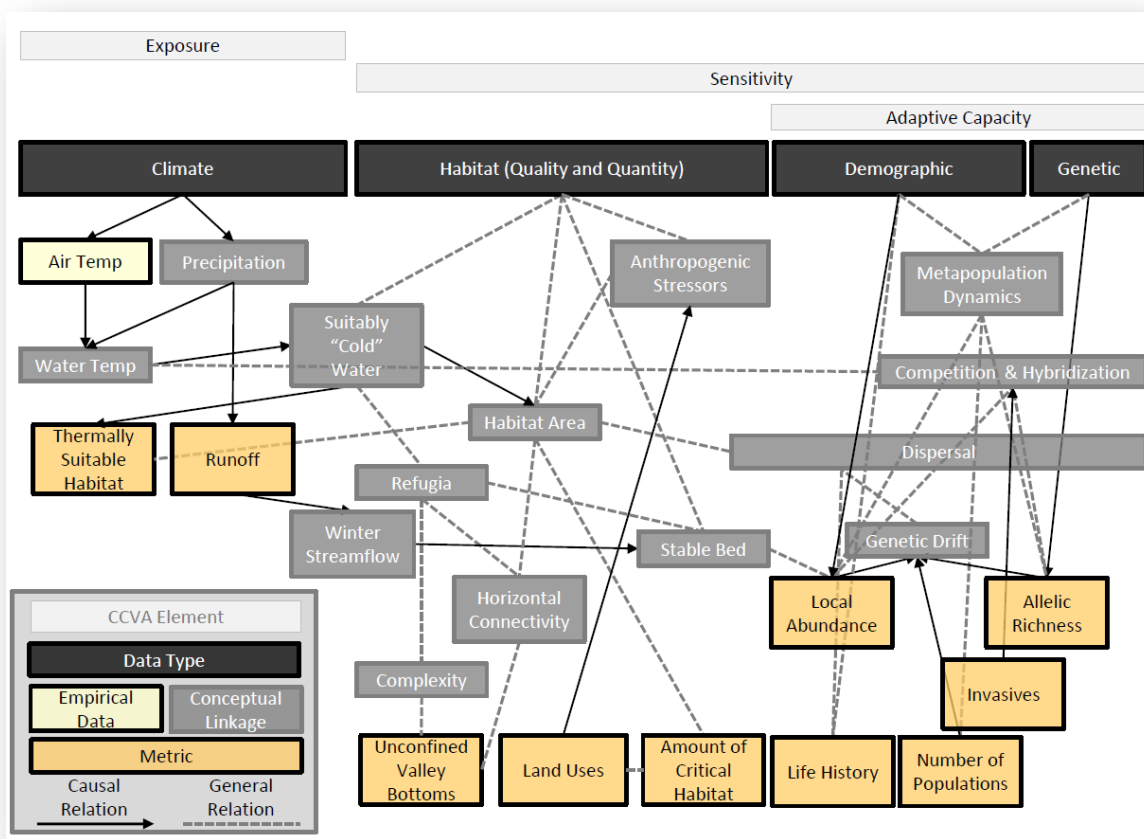


Fig. 8. Conceptual model for a bull trout CCVA including the major elements (exposure, sensitivity, and adaptive capacity) further broken down into species specific indicators that can be categorized under climate, habitat, demographic or genetic.

Overall, steelhead showed less range in metapopulation vulnerability rating as compared to bull trout (Fig. 9 and Fig. 10, right panels). There also appeared to be little difference in vulnerability between winter and summer run metapopulations. Our sensitivity analysis results for steelhead indicated that inclusion of abundance (D) tended to reduce vulnerability ratings on average compared to the full model for summer run steelhead (avg = 6.67, SD = 7.5) and winter run steelhead (avg = 6.48, SD = 11.2). For summer run steelhead, the simple genetic model (E + G) was on average higher than the full model with high variation in vulnerability ratings (avg = -3.69, SD = 13). This further lead to a larger average difference in the vulnerability rating as predicted by the simple demographic and genetic models for both summer run (avg = 10.4, SD = 18) and winter run steelhead (avg = 6.4, SD = 18.8).

Conclusions

Our analysis demonstrated the importance of considering a range of available data including environmental, demographic and genetic data when conducting CCVAs. Interestingly, though there was overall little average difference between the vulnerability ratings calculated in the simple genetic or simple demographic models, the variation was large. This can lead to largely differing results in vulnerability ratings for independent metapopulations. Further, it can potentially lead managers to draw very different conclusions about how to prioritize management and mitigation based solely on data availability (or the lack thereof). This result was best illustrated in steelhead where high variation in the differences between simple models (exposure with the addition of genetic or demographic metrics) might lead to potentially very different metapopulation ratings. Including more diverse datasets is also likely to better represent all three vulnerability elements including exposure, sensitivity and adaptive capacity, the last of which is often ignored in CCVAs or implicitly assumed in other less appropriate metrics.

Management Implications

A major advantage of using a multi-species CCVA (and CCVAs in general) is the ability to relatively rank and prioritize populations most at risk. Comparison of CCVA elements informs on the robustness of CCVA results across hypothesized controls on population vulnerability and guides managers in appropriate inferences from CCVA results. Here, our results can be used to better guide both monitoring (e.g., gathering population and genetic trend data to test vulnerability estimates) as well as guide preliminary conservation action prioritization in steelhead and bull trout. For example, in steelhead, we noted a trend for genetic data to increase the vulnerability rating (i.e., negatively impact) of many populations while markedly lowering (i.e., improving) the rating of a few metapopulations. The high variation in vulnerability ratings is of importance because managers, who rely solely on demographic or genetic data, may be incorrectly prioritizing populations based on one source of data alone. Thus, we stress the need for managers, as supported by our results, to better consider multiple sources of available data that cover a wide range of potential information including at the least metrics representing environmental conditions and change, demography and genetic diversity (and connectivity).

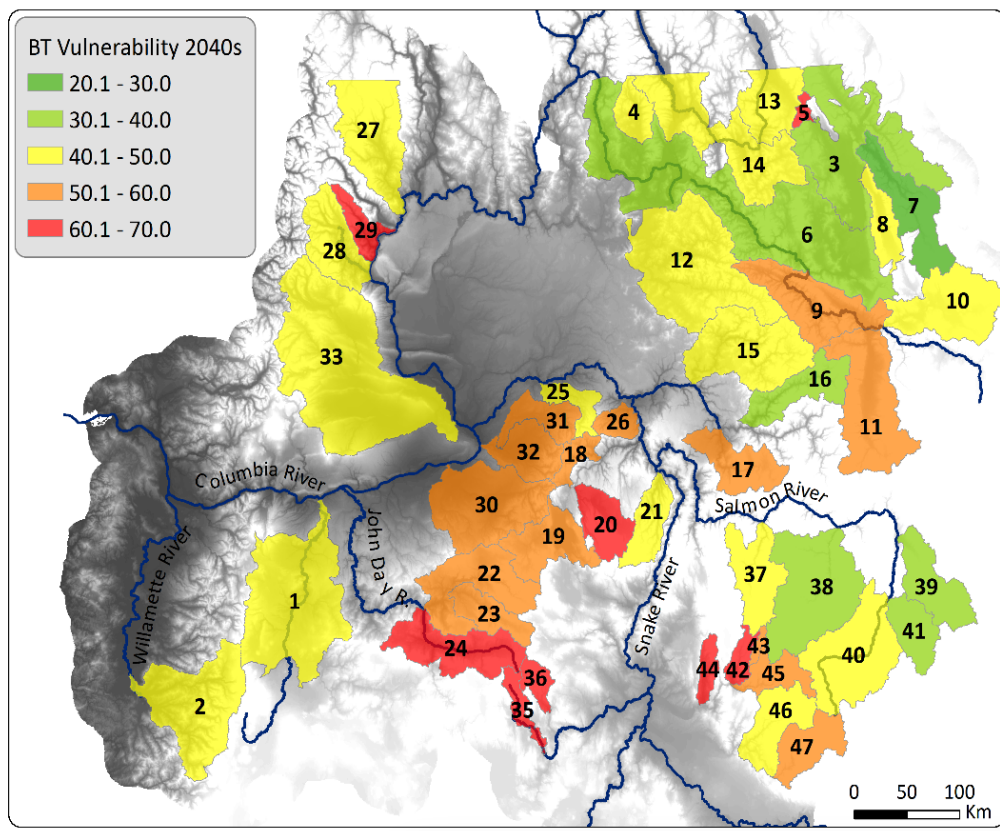
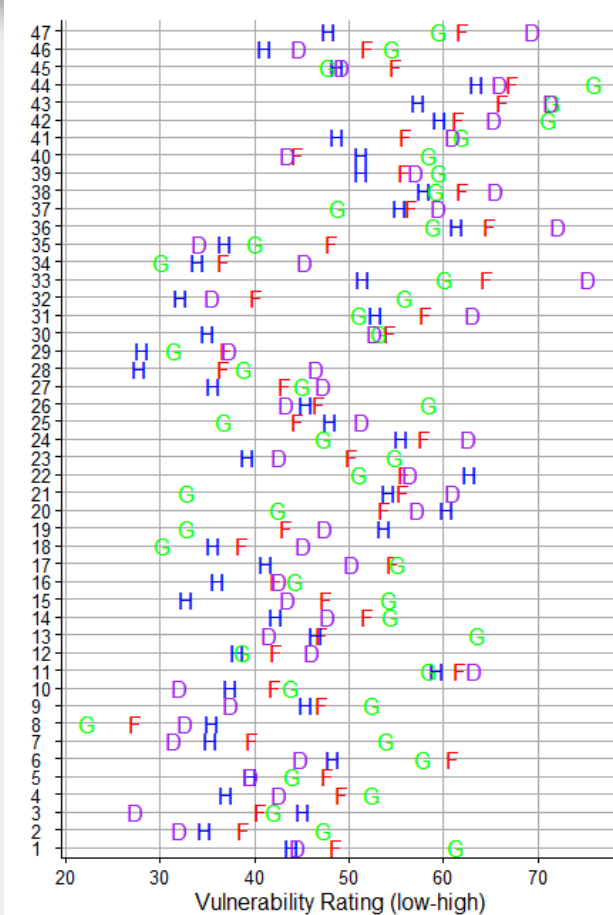


Fig. 9. (Above) Climate Change Vulnerability Assessment (CCVA) results for bull trout throughout the Columbia River Basin. Colors (green – orange) represent increasing vulnerability to future and current threats. (Right) Sensitivity analysis conducted for each numbered metapopulation in the above CCVA illustrates how varying the types of stressors assumed to increase steelhead population vulnerability shifts the resulting level of vulnerability. F = “full model” of exposure + habitat + demographic + genetic metrics included in the CCVA; H= exposure + habitat; G = exposure + genetics; D = exposure + demographics.



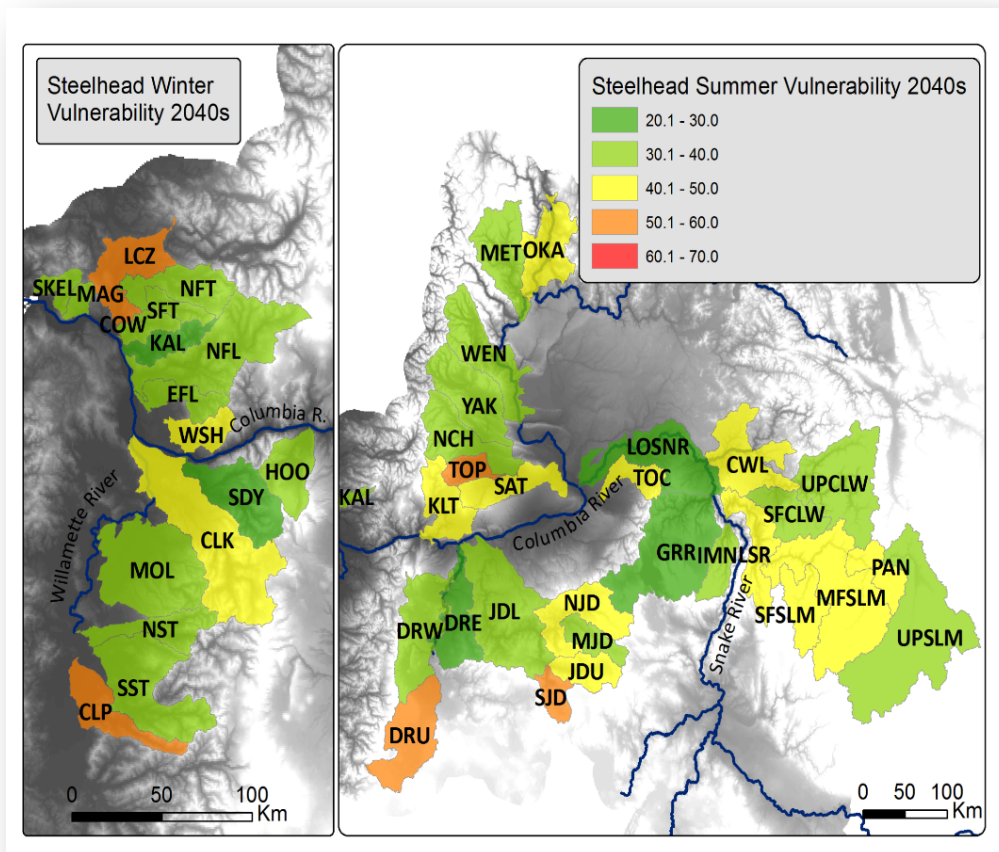
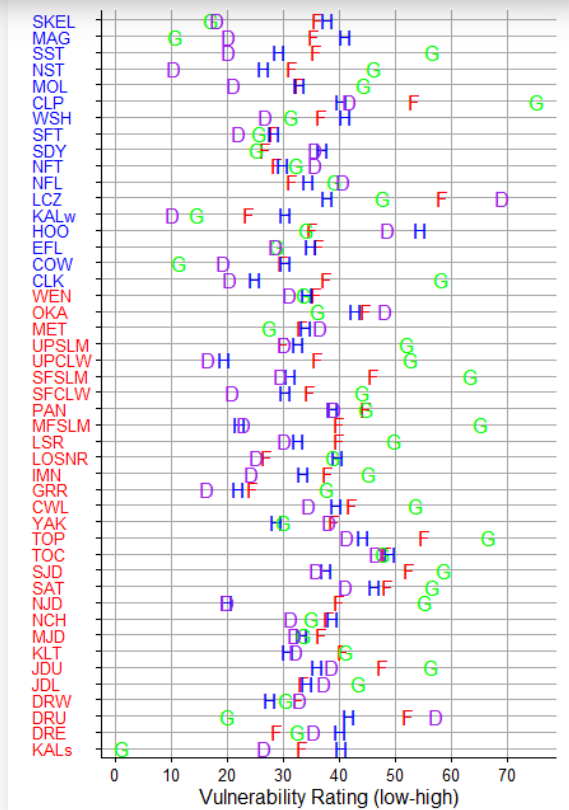


Fig. 10. (Above) Climate Change Vulnerability Assessment (CCVA) results for (winter and summer run) steelhead throughout the Columbia River Basin. Colors (green – orange) represent increasing vulnerability to future and current threats. (Right) Sensitivity analysis conducted for each steelhead metapopulation in the above CCVA illustrates how varying the types of stressors assumed to increase steelhead population vulnerability shifts the resulting level of vulnerability (blue = winter run, red = summer run). F = “full model” of exposure + habitat + demographic + genetic metrics included in the CCVA; H= exposure + habitat; G = exposure + genetics; D = exposure + demographics.



Objective 6: Explore, conceptualize and develop a framework that applies a more holistic, landscape community genomic approach to help advance conservation science and management.

Hand, Brian K., Winsor H. Lowe, Ryan P. Kovach, Clint C. Muhlfeld, Gordon Luikart. 2015.

Landscape community genomics: understanding eco-evolutionary processes in complex environments. *Trends in Ecology and Evolution*. In Press.

Summary

Extrinsic factors influencing evolutionary processes are often categorically lumped into interactions that are environmentally (e.g., climate, landscape) or community driven, with little consideration of the overlap or influence of one on the other. However, genomic variation is strongly influenced by complex and dynamic interactions between environmental and community effects. Failure to consider both effects on evolutionary dynamics simultaneously can lead to incomplete, spurious, or erroneous conclusions about the mechanisms driving genomic variation. Under this objective we highlighted the need for a Landscape Community Genomics (LCG) framework to help motivate and challenge scientists in diverse fields to consider a more holistic, interdisciplinary perspective on the genomic evolution of multi-species communities in complex environments.

Purpose and Objectives

The analogy of the “ecological theater and the evolutionary play” has been present in the scientific literature for at least the past five decades (Hutchinson 1965). In recent years, there has been renewed emphasis on the importance of resolving the interplay between the ‘actors’ and the ‘stage’ that create the evolutionary play (i.e., interacting species and the abiotic environment in which those interactions take place; Pelletier et al 2009; Post and Palkovacs 2009). Explicit consideration of the simultaneous, interactive effects of both biotic and abiotic impacts on evolutionary processes, however, has not been fully incorporated in contemporary approaches aimed at elucidating patterns of genomic variation in populations, species, and ultimately communities. Specifically, the burgeoning field of landscape genetics interprets patterns of genetic divergence and diversity based primarily on abiotic or physical variation, whereas community genetics interprets those patterns based on interactions among species

(Whitham et al 2003; Manel et al 2003). This relatively narrow focus on either abiotic or biotic drivers of genomic variation is understandable given the past limitations of genetic tools. Fortunately, recent advances in genomic techniques make it feasible to consider the simultaneous influence of the abiotic ‘stage’ and biotic ‘actors’ on the ‘evolutionary play’. Our goal under this objective was to show the need for this conceptual shift by introducing a novel “Landscape Community Genomics” (LCG) framework that merges a diverse set of sub-disciplines in evolutionary biology and ecology.

Approach

Landscape community genomics (LCG) is the study of how neutral and adaptive genomic variation within and among populations of interacting species is shaped by both abiotic and biotic factors across diverse landscapes. LCG is distinct from other approaches in that it explicitly tests whether patterns of genomic variation in multiple species vary as a result of inter-specific interactions and whether these interactions vary across landscape or environmental gradients. In other words, LCG attempts to quantify the effects of eco-evolutionary processes occurring across complex environments where selective pressures, gene flow, and genetic drift interact in time and space. This includes genome x genome interactions (e.g., hybridization, antagonistic or mutualistic co-evolution, etc.), genome x environment interactions (e.g., parallel adaptation, demography, dispersal, etc.) and, ultimately, genome x genome x environment interactions (e.g., context-dependent interactions among species, environmental conditions, and resulting evolutionary dynamics) that shape patterns of neutral and adaptive genetic variation.

LCG brings together a rich history of approaches in genetics and ecology, including foundations in population genetics, landscape ecology, and community ecology. With such a robust theoretical foundation, the recent explosion in genomic sequencing could prove to be the necessary catalyst in unraveling the complex interactions of geography, ecology, and evolution shaping the genomes of entire communities of species, thus opening the curtain on a new and exciting act in the evolutionary play.

What types of data and sampling are useful in LCG?

LCG studies focus on multiple interacting species distributed along landscape or environmental gradients. Fundamentally, these studies require three distinct data sets: genomic data on the focal species, ecological data on those species (e.g., occurrence, abundance), and

environmental data across the study area. Even with these data, landscape level eco-evolutionary dynamics are challenging to causally attribute to key biotic interaction or environmental variation because both species interactions and environmental conditions vary spatially and temporally (e.g., context-dependence or environmental gradients). Partly, the solution requires capitalizing on genetic and ecological data sources (e.g., measures of demographic connectivity to complement measures of genetic connectivity; Lowe and Allendorf 2010), but it also requires strategic sampling across abiotic and biotic environments.

Ideally, ecological and environmental data—the independent variables in LCG models—should be spatially (and if possible, temporally) diverse to capture strong environmental gradients and key moments in community structure and function (e.g. before and after a disturbance event, introduction of an invasive species, or colonization of novel habitat). Replication across biotic and abiotic gradients is critical to correctly identify drivers of genomic diversity, as community composition is also a direct result of environmental processes, thus further complicating our ability to correctly identify the sources of abiotic and biotic variation influencing genomic diversity. Often, this will require combining genomics data (individual, population, and community level) with modeled or remotely sensed climatic and landscape data to identify environmental drivers of genomic variation and fine-scale data on community composition, abundance, or occurrence patterns of interacting species. Gathering the necessary fine-scale data is not trivial, which might partially explain the emphasis on geographic and abiotic variables in most landscape genetic studies. However, these data are crucial to advance understanding of how landscape × community interactions shape genomic variation within and among species.

Additionally, the LCG approach requires identifying candidate adaptive genes controlling local adaptation in the focal species, preferably with known or potential effects on species interactions (Whitham et al 2006). Future research can capitalize on recent genomic advancements that are key to the emerging field of LCG, and are providing unprecedented opportunities to study genome-wide markers under selection in multiple non-model species. Novel exon capture techniques, for example, allow targeted sequencing of areas in or near genes of known or suspected function, allowing for capture of neutral and adaptive gene markers (Cosart et al 2011). Targeted sequencing of exons is also useful for LCG because multiple divergent species can be sequenced for the same exons (Cosart et al 2011). Various forms of RAD sequencing (Restriction site associated DNA sequencing) can be applied to any non-

model species because it requires no genomic resources (Andrews et al 2014). A relatively inexpensive version of RAD-seq is targeted capture of thousands of informative (highly polymorphic) RAD loci, which can cut costs and thereby facilitate multispecies LCG studies (Andrews and Luikart 2014). Finally, metagenomic techniques are potentially a useful genetic technology for LCG-type studies in the future because these techniques offer the ability to yield DNA sequences for multiple species simultaneously (Allendorf et al 2013).

Conclusions

Landscape genetics and community genetics have developed as largely independent disciplines, growing in popularity and importance, but without capitalizing on the complementary nature of the two approaches. Intuitively, however, we know that natural systems are comprised of multiple species that interact and exist in highly variable abiotic environments. We believe that combining landscape and community genetics approaches and perspectives is crucial to illuminating the factors driving eco-evolutionary processes occurring within ecosystems and across landscapes. The recent explosion in genomic sequencing and genotyping techniques—applicable to any species—will help biologists to exploit the enormous potential of LCG approaches. Not only does the LCG approach and perspective represent an exciting frontier in the integration of basic evolutionary and ecological research, it is also a crucial tool for understanding how interrelated and accelerating rates of biodiversity loss and global environmental change will affect the evolutionary trajectory of species and natural communities.

Management Implications

LCG offers a new dimension in conservation management by broadening our understanding of how current and future change might impact evolutionary processes at the community and ecosystem scales. Maintaining populations and their adaptive potential requires preservation of life history variation, connectivity corridors among populations, and genetic variation within and among populations. Thus, most conservation strategies have focused on reducing vulnerability (i.e., sensitivity and exposure) to climate and human stressors, increasing adaptive capacity (i.e., resiliency), and anticipating and facilitating ecological transitions (e.g., range shifts and resulting species addition or loss) that are caused by the changing environmental conditions (Glick et al 2011).

Clearly, genetic data are valuable for advancing our understanding of species and community vulnerability to local environmental conditions and shifts in those conditions, but there are very few instances where genetic data have been used in this context, especially for multiple interacting taxa. Genetic structure and diversity represent species' sensitivity and adaptive capacity, both of which are key elements of assessing vulnerability of populations (Solomon et al 2007). The more holistic approach offered by LCG can better inform vulnerability assessments over large, ecologically diverse landscapes, which is increasingly important for conservation efforts that seek to increase resiliency in natural ecosystems, maintain important eco-evolutionary dynamics, and avoid biodiversity loss.

LCG can also offer insight into eco-evolutionary relationships among native and non-native species. For example, hybridization (or the lack thereof) arises from localized interactions between species, yet is often viewed as a consequence of co-occurrence alone (i.e., if species occur together and can interbreed, they will), which places the emphasis on abiotic and spatial predictors of co-occurrence. However, like other ecological interactions, the localized interactions that promote or prevent hybridization are context-dependent. There is growing evidence that hybridization dynamics can be influenced by interactions between community and environmental sources of selection, ultimately resulting in complex patterns of genetic admixture and adaptive evolution (Fitzpatrick et al 2010; Muhlfeld et al 2014). LCG gives us the framework to identify how abiotic and biotic drivers affect hybridization rates among species whether naturally sympatric or allopatric. Adaptive introgression, for example, has been shown to counteract anthropogenic habitat change (e.g., the use of insecticide to control mosquito vectors of malaria was counteracted by introgression of insecticide resistance genes from one mosquito species into another; Clarkson et al 2014). Adaptive introgression is also of interest because of the role it plays in shaping genome-wide patterns of invasive admixture in species of conservation concern (Fitzpatrick et al 2010; Hohenlohe et al 2013).

Objective 7: Assess potential socioeconomic impacts of potential climate warming on cutthroat trout.

Duffield, John and Chris Neher. 2014. **Modeling climate change economic impacts to a recreational trout fishery: Upper Flathead River, Montana**. Manuscript. Department of Mathematical Sciences, University of Montana, Missoula, 59812.

Summary

This research is part of a larger project with the overall goal of determining effects of climate change on salmon and trout habitat and population vulnerability. This was an integrated ecological-economic study that aimed to describe impacts in both biological and economic metrics. The focus of the economics team was on assessing the potential socioeconomic impacts of potential climate warming on cutthroat trout. We utilized the findings of the ecological team in objective 2, which focused on developing a demogentic modeling framework to assess impacts of climate change on salmonids, using threatened bull trout as a case system (Jones et al 2014). Because cutthroat have similar temperature thresholds to bull trout, climate related impacts on cutthroat populations were available. We used two metrics from the ecological work, cutthroat presence (river sections targeted by anglers for cutthroat) and trout biomass. These metrics provided a link of the ecological findings to a spatially explicit economic model of sportfishing in Montana. This random utility travel cost approach allowed us to model angler behavior in response to reduced availability of cutthroat trout in four river sections of the Upper Flathead. The primary finding is that the increasing absence of cutthroat trout (modeled at years 2059 and 2099 and interpolated from a year 2000 baseline) and a 50% reduction in trout biomass in the Upper Flathead would have a present value loss of \$116 million in 2010 dollars. This estimate is in a benefit-cost accounting framework. One could also estimate the regional economic impacts based on the predicted reduction in angler trips to these sites. The contribution of this work is to demonstrate a way to link ecological metrics from climate change impacts on natural systems to a model of an economically important human system, sportfishing in Montana. The work to date is more of a proof of concept than a definitive empirical estimate, and is likely to be quite a conservative estimate. It would be feasible to use these types of estimates to inform management and conservation decisions, such as evaluating the cost effectiveness of controlling source populations of invasive species (e.g. rainbow trout) to protect the remaining cutthroat populations in these systems.

Purpose and Objectives

The goal of the economic team was to quantify the economic loss associated with the decline in salmonid habitat as projected out to 2099. The Flathead River System is an important sport fishery; in the river system the primary target is the west slope cutthroat trout. We utilized

a prior Montana resident angler data set and modeling effort in Montana that was focused on identifying the impacts of mining and toxic metals on the river fisheries downstream of the historic mining centered around Butte, Montana. We estimated a new state-level model that included not only trout biomass but also presence/absence of cutthroat trout as drivers of angler use, using a spatially explicit (random utility travel cost model) framework that links angler residence (origin) locations to river destination sites. This model has the capability of modeling angler response to changes in site characteristics including trout biomass and species availability but access and other site characteristics as well as individual angler characteristics (e.g. income, age, resident/nonresident status, etc). The angler data indicates that almost all angler pressure is in the forks and main stems of the river system, in other words in the foraging, migrating and overwintering habitat as opposed to the spawning and rearing habitat in the tributaries.

The spatial extent of the economic sportfishing model is necessarily much larger than the Upper Flathead River System study area and includes all of the trout-fishing waters in the State of Montana. This is necessary to more fully represent the substitute sites available to anglers that allow them to minimize their loss from the projected diminished quality of the study area rivers.

Approach

The economic work is entirely dependent on the ecological characterization of changes in the natural systems. The economics adds a model of human behavioral response (in this case by sportfishers) in adapting to changes in fishery quality and biodiversity. The economic model includes 38 lake sites and 62 river sites, including the four Montana Department of Fish, Wildlife and Parks sites defined in the study area: the upper mainstem Flathead river, and the North, South, and Middle Forks of the Flathead. The angler random utility model (RUM) is limited to resident anglers. We estimate foregone nonresident (out of state) angler loss based on the historical relationship of resident and nonresident angler use in Montana and the relationship of trout populations to angler pressure at the site level. Additionally we identify the net economic loss to non-angling recreators such as family members who accompany anglers on fishing trips based on prior angler surveys.

Because bull trout are a listed species for which angling is not permitted, we focused our analysis on cutthroat trout, which are the primary target species in the study site. Because

cutthroat have a very similar thermal tolerances to bull trout, we utilized the Jones et al (2014) findings on FMO habitat loss estimates briefly summarized above. We assumed that biomass changes (population per 1000 feet of stream) are proportional to habitat loss. We further assumed that after a 50% decline in habitat these streams would no longer be specifically targeted by anglers for cutthroat.

Results

As noted, the economic findings are dependent on the estimates developed through the demogentic modeling work. The primary findings of the ecological work are summarized in Jones et al (2014), including an empirical application to the Flathead River Basin, USA and Canada. Spatial and nonspatial models were parameterized to predict August stream temperatures (22-m resolution) throughout the study area. A spatial hierarchical model was used to estimate thermal regimes for threatened bull trout habitats. The model estimated summer thermal regimes of spawning and rearing (SR) habitats at < 13 degrees C and foraging migrating and overwintering (FMO) habitat at < 14 degrees C. To illustrate application of the model, climate warming scenarios were simulated to quantify potential loss of critical habitat under forecasted climatic conditions. As air and water temperatures continue to increase, the model simulations show that the lower portions of the Flathead River basin drainage (FMO habitat) may become thermally unsuitable and headwater streams (SR habitat) may become isolated because of thermal fragmentation during summer.

The ecological team estimated August average temperatures using three different climate general circulation models, with associated lowest, “conservative”, and highest warming scenarios, respectively. For example, the “conservative” model 21st century climate simulations predict that August summer air temperatures in the study area will rise by 3.6 degrees C between 2000 and 2059 and by 6.1 degrees C between 2000 and 2099. Driven in part by air temperatures, the stream temperature model estimated 97.9 % of August FMO habitat at water temperatures below the 14 degrees C threshold for bull trout. The “conservative” climate model-based estimate for bull trout habitat loss in the study area is a potential 58% loss of FMO habitat by 2059 and an 86% loss of FMO habitat by the end of this century (2099).

The economic model links to the ecological outcomes through metrics for presence/absence of cutthroat and trout biomass. The economic model provides estimates of the change in trips at the four study sites as well as sites throughout Montana, as anglers

respond to declining quality (absence of cutthroat, decline of trout populations) at the Flathead sites by choosing substitute sites to fish, generally near to their homes throughout Montana; some anglers also choose to not fish. At a 50% loss of habitat, for example, resident trips taken decline by about 3,500 out of a baseline estimated in year 2000 at 11,000 in the North Fork, by about 2,500 out of a baseline of 8,200 in the Middle Fork, by about 1,000 out of 2,000 in the access-limited South Fork (almost entirely contained in the Bob Marshall Wilderness Area), and by about 20,000 trips out of a baseline of 48,000 angler trips per year in the upper Flathead mainstem between the forks and Flathead Lake. However, the net trip loss in this scenario is only 3,872 because while some anglers take fewer trips, most anglers now switch to fishing substitute sites such as the Swan Lake, Hungary Horse Reservoir, Flathead Lake, and Lake Koocanusa, Kootenai River, Stillwater, and Whitefish Rivers. The net economic loss to Montana resident anglers from projected climate change-related reduced fishing opportunity in the upper Mainstem Flathead River and Forks in 2059 amounts to \$1.8 million per year in 2014 dollars. With the addition of related losses to nonresident anglers and non-angling travel party members, losses per year are around 5.0 million.

Interpolating between the estimated losses at baseline, in 2059, and 2099, the net present value of the stream of climate-related losses at the four Upper Flathead River sites in the study area totals 116 million at a 3% real discount rate.

The estimate of \$116 million present value is under the assumption that cutthroat trout are, after 50% or more loss of cutthroat habitat, not longer targeted by anglers in a given river section and that trout biomass is reduced by 50% at the four Flathead River sites. We also modeled just the effect of the cutthroat presence/absence and assumed no change in biomass; the cutthroat loss alone accounts for 79.47% of the total loss or approximately \$92.2 million. Further research could explore the implications of hybridization by rainbow in these reaches and the net effect on trout biomass. For example, if rainbow or hybrid populations replace cutthroat in these rivers, perhaps trout biomass will be relatively stable and losses more on the order of a conservative \$92.2 million.

Conclusions

This study demonstrates the feasibility of linking climate change-related ecological outcomes to a spatially explicit economic model of angler behavior. The specific findings here must, however, be regarded as preliminary rather than definitive. Among other limitations,

there is considerable uncertainty across the general climate models that we have not carried through to the results. The results may well be overly conservative because we incorporate ecological changes only for the four study sites when in reality, it is likely that any such impact would not be limited only to the Flathead system. Rather, impacts on trout populations would also be seen in other nearby waters. For this reason, the results presented are conservative, as the model as specified assumes no degradation in the attractiveness of waters outside the Upper Flathead System. This allows these waters to serve as unimpaired substitutes within the model structure. A more realistic scenario would likely also show trout population impacts in adjacent waters. In other words, the relevant spatial scale of the economic behavior model is across the primary “market” for fishing sites, in this case most of the State of Montana. However, the ecological work is at a much smaller spatial scale. Future research could remedy this mismatch.

The current work was limited to what could be feasibly undertaken given existing data sets. The economic data set available is somewhat dated (1992) but provides an approximation to the baseline (year 2000) and projected year fisheries. Some stability is provided by relative consistent availability year to year of fishing opportunities across Montana lakes and rivers, as well as the relatively stable distribution of angler residence locations across Montana cities and towns.

Management Implications

The basic accounting framework used in the current study is the benefit-cost framework, which essentially measures all costs and benefits including both market and nonmarket values. This is especially relevant in an analysis of a sportfishery in that much of the value is not observable in actual market transactions (such as buying gas or food for the trip or hiring a fishing guide), but rather is the net benefit to the angler over and above the amount he or she actually pays in costs to undertake the trip. The availability of net economic benefit (loss) estimates related to climate change provides a very flexible tool for undertaking benefit-cost evaluation of any of a number of conservation and climate-mitigation strategies. It was beyond the scope of the current effort to investigate the technical feasibility or costs of any such allocations or strategies, but this would all be quite feasible. One obvious analysis would be to evaluate the prior work by Montana Fish Wildlife and Parks to control source populations of

rainbow trout in these systems which are expanding into and hybridizing with cutthroat in the Upper Flathead, including waters adjacent to and inside Glacier National Park.

An alternative complementary accounting framework is to undertake a regional economic analysis to identify (not just benefits and costs) but also impacts on jobs, income, and related economic metrics that measure the health of the regional economy centered on the Flathead. Since the random utility travel cost model effort identifies the change in trips it is readily feasible to also identify changes in their costs and related market transactions, and how these impact the regional economy in terms of personal income and jobs. Such an extension would be readily feasible in future research through application of a Leontief-style input output modeling effort.

Other considerations for future research includes also investigating potential regulatory linkages between fishery habitat and demographics that might complement or supersede the more direct linkage of angler behavior and fish biomass and diversity. For example, stream temperature-related closures to protect trout fisheries are already occurring in Montana, for example during late summer on the Blackfoot and Bitterroot Rivers. A systematic model could be developed that links stream temperature to fishery closures. It is also possible that long-term elevated stream temperatures and related hybridization and other impacts could lead to listing of cutthroat as an ESA species and associated limits on sportfishing that parallel current limits on targeting bull trout.

A final note concerns the stability of angler pressure in the region. The model as estimated also conservatively assumes that there is no baseline growth in angler use of waters in the region into the future (absent trout population impacts). Data from Montana DFWP suggest that a more realistic assumption would incorporate a long-term growth factor for baseline angler pressure in the net present value calculations of angler WTP losses

10. OUTREACH:

RAP improvements: A decision support tool for managers

The original RAP website (rap.ntsg.umd.edu) was substantially updated to further develop it into a prototype Decision Support System (DSS). Our redesigned focused on improving user-friendliness and accessibility and the addition of information describing Climate Change Vulnerability Assessments (CCVAs), riverscape genetics and demogenetic monitoring and links for users to participate in citizen science. Individual web pages provide end-users with educational resources through case-study examples and additional links for users to further explore publications related to each of the major tools.

New to our remote sensing metrics database, we have developed additional tools that aid end users in extracting metrics related to temporal dynamics in freeze thaw (FT), inundation, and mean annual net primary productivity (NPP). The new FT tools (processed from NASA MEaSUREs FT-ESDR [Kim et al. 2011]) can be used to define climatological timing and duration of the non-frozen season as a proxy for potential productivity and ice-free aquatic habitat accessibility. The inundation data are derived from AMSR-E (Jones et al. 2010; Watts et al. 2012) and provide seasonal climatology of riparian inundation dynamics, used as a proxy for aquatic

habitat connectivity.

Finally, NPP estimates (from the MODIS MOD17 operational product) provide spatially contiguous, landscape-level predictions that serve as a proxy for upland terrestrial productivity of aquatic foodwebs (Oberdorff et al. 2011). These synergistic datasets provide new

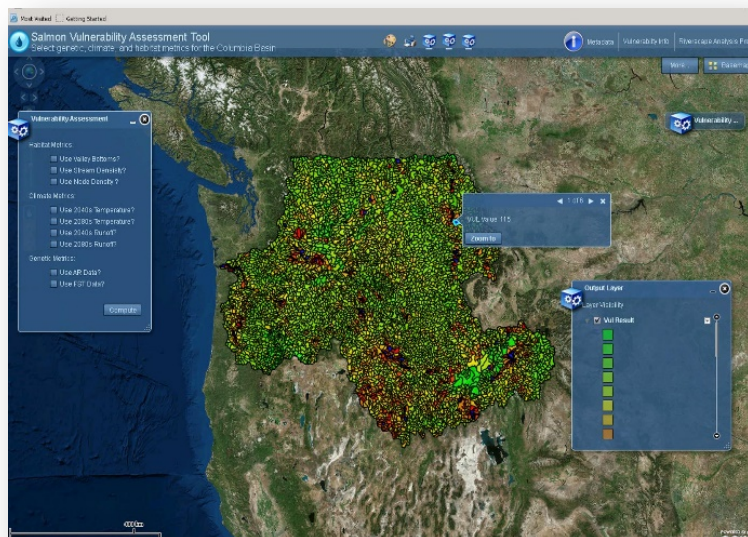


Fig. 11. Screenshot of the prototype CCVA tool from the RAP website.

physical habitat metrics that govern the timing and duration of effective habitat use, productivity, and connectivity. In addition, they provide a means for assessing dynamic habitat impacts from recent climate change and insight on how and where critical habitats may be vulnerable to future climate change.

A major outcome of objective 5 in this report is the development of a web-based CCVA tool from our CCVA analysis of bull trout and steelhead in the CRB that will be used as case examples for the web-based tool, but will also serve as a jumping off point for managers to use our compiled datasets to conduct further CCVAs for their watersheds of interest. Further, we expect this tool to be continuously developed into the future with additional datasets (e.g., demographic, genetic, environmental, etc.) and extended to additional salmonids. The analysis conducted in objective 5 (and this project) were invaluable for initiating the development of these important tools aimed at conservation management and monitoring. In addition, an interface for the CCVA toolset is currently in development (Fig. 9). We will continue to finalize integration of prototype components of the CCVA, riverscape genetic and demogenetic monitoring tools in the near future (funding dependent). The prototype CCVA toolset will be available publicly with steelhead and bull trout example data for CCVAs when finished; prototype riverscape genetic and demogenetic tools will follow in the upcoming year.

Applied Research and Management

This project's results directly benefited resource managers throughout the Columbia River Basin and Rocky Mountains of the USA and Canada. The following are the names of agencies and agency personnel that we worked with through this project, including specific management actions and decisions that were informed by our research results and products.

- **Crown Managers Partnership (CMP), USA and Canada:** In November 2014, the CMP and its partners sponsored a workshop "*Taking Action on Climate Change Adaptation: Piloting Adaptation Strategies to Reduce Vulnerability and Increase Resilience for Native Salmonids in the Crown of the Continent Ecosystem*", held in Kalispell, MT. Forty-five participants from 20 state, federal, provincial agencies, tribes, nongovernmental conservation organizations, universities, community groups, as well as six large-landscape collaboratives and initiatives participated in the three-day workshop. The goal was to collaboratively identify geospatially-explicit adaptation strategies and tactics to reduce vulnerability and increase resilience for bull trout and westslope

cutthroat trout across the CCE. The workshop used our NWCSC and GNLCC-funded projects to deliver landscape-scale climate change and vulnerability science products as a basis for establishing where shared resources could be effectively used to advance Crown-wide climate adaptation projects for threatened bull trout and westslope cutthroat trout. We provided a comprehensive overview of the status and trends for each species and projected impacts of climate and non-climate stressors to set the context for climate adaptation planning. Additionally, we shared downscaled, regional climate models and climate data available for the Crown, as well as our stream temperature modeling and monitoring results for the CCE. Specifically, maps were used to identify potential thermal refugia (e.g., cold water streams, groundwater upwelling zones) for various climate scenarios and to identify potential habitats in the CCE that may exceed thermal preferences of bull and cutthroat trout. Last, we demonstrated how these results could be used to focus conservation efforts (tactics) by a wide range of agencies, landowners, and partners, including measures to: restore and enhance connectivity; reduce/eliminate nonnative species (where feasible); restore and protect critical habitats (streams, lakes, riparian/upland areas) and populations; maintain instream flows and temperatures; implement restrictive angling regulations where/when necessary; collaborate across borders and jurisdictional boundaries; develop adaptation plans for focal species; and monitor populations and aquatic habitat conditions.

- **National Park Service, Glacier National Park.** Chris Downs, Fisheries Biologist, and Phil Wilson, Natural Resources Manager. Managers were considering various alternatives to protect unique native species strongholds through construction of upstream fish passage barriers in two watersheds, while also seeking to minimize potential impacts to life history diversity and long-term persistence of native salmonid populations. This project provided spatially explicit predictions of current and future climate change (e.g., stream temperature), spread of invasive species, and demogenetic data to assess trade-offs of barrier placement scenarios. Our results helped managers make informed decisions for placing two barriers in GNP for conservation of remaining native trout populations. Our results also were used to identify areas of targeted suppression of non-native rainbow trout and lake trout, which have caused significant declines of native bull and cutthroat trout in GNP.

- **U.S. Fish and Wildlife Service.** Wade Fredenberg, Fisheries Biologist and Bull Trout Recovery Planner. Our project assisted the FWS with assessing the vulnerability of threatened bull trout across the Columbia River Basin for recovery and management planning. Specifically, our project produced estimates of current and future climatic conditions (e.g., stream temperature and flow), habitat conditions, and patterns of genetic diversity in 130 bull trout populations from 24 watersheds across the CRB. Results showed that over the next century, stream habitats will warm and stream flows will become more variable across the Columbia River Basin, yet bull trout populations that will need to adapt the most to these changes may have the lowest adaptive potential because they have the lowest amounts of genetic diversity. Our results will help managers increase resiliency and adaptive potential in vulnerable populations by reducing existing stressors, such as restoring and reconnecting cold, clean and complex habitats, and reducing impacts of invasive species. Our results will also be used for recovery planning.

Publications

Hand, Brian K., Winsor H. Lowe, Ryan P. Kovach, Clint C. Muhlfeld, and Gordon Luikart. 2015. Landscape community genomics: understanding eco-evolutionary processes in complex environments. *Trends in Ecology and Evolution*. In Press.

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Presentations

Brian K. Hand, Gordon Luikart, and Clint Muhlfeld. A metapopulation studying using riverscape genetics models for salmonids across Pacific Northwest. Montana Chapter of the American Fisheries Society, Chico Hotsprings, Montana, March 2014.

Ryan Kovach, Clint C. Muhlfeld et al. Invasive hybridization in a threatened species is accelerated by climate change. Coastwide salmonid genetics meeting. Juneau, Alaska. June 2014.

Clint C. Muhlfeld. Impacts of climate change on aquatic ecosystems in the Crown of the Continent. National Wildlife Federation Seminar. Kalispell, Montana. 30 October 2013. INVITED SPEAKER

Clint C. Muhlfeld. Aquatic biodiversity in the Crown: Scale and context matter. Crown Managers Partnership Landscape Patterns Workshop. Fernie, British Columbia. 16 January 2014. INVITED SPEAKER

Clint C. Muhlfeld. Invasive hybridization in a threatened species is accelerated by climate change. Montana Chapter of the American Fisheries Society Annual Meeting. Chico, Montana. 5 March 2014. SPEAKER

Clint C. Muhlfeld. Climate change effects on aquatic ecosystems in the Crown of the Continent: Implications for adaptive management. Crown Managers Partnership Annual Forum. Fernie, British Columbia. 17 March 2014. INVITED SPEAKER

Clint C. Muhlfeld. Invasive hybridization in a threatened species is accelerated by climate change. Western Division of the American Fisheries Society Annual Meeting. Mazatlan, Mexico. 8 April 2014. INVITED SPEAKER

Clint C. Muhlfeld. Invasive hybridization in a threatened species is accelerated by climate change. North American Congress for Conservation Biology Annual Meeting. Missoula, Montana. 14 July 2014. SPEAKER

Clint C. Muhlfeld. Assessing the potential impacts of climate warming on aquatic ecosystems in the Crown of the Continent: implications for adaptive management. North American Congress for Conservation Biology Annual Meeting. Missoula, Montana. 15 July 2014. INVITED SPEAKER

Clint C. Muhlfeld. Native salmonids across the Crown: Available science to inform decision-making. Crown Managers Climate Change Adaptation Workshop. 18 November 2014.
http://crownmanagers.org/storage/Muhlfeld_Jones_CCE_workshop_2014_combined%20copy.pdf

Clint C. Muhlfeld. Predicting climate change impacts on native salmonids across the Pacific Northwest. DOI Climate Change National Webinar. 2 December 2014.
<https://nccwsc.usgs.gov/webinar/355> INVITED SPEAKER

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Media

Newspaper

- High Country News: June 6, 2014: [Climate change expedites hybrid trout takeover](#)

- Columbia Basin Bulletin: May 30, 2014: [Study Finds Climate Change Accelerates Hybridization Between Native, Invasive Trout](#)
- Daily Interlake: May 30, 2014: [Study: climate change has boosted fish cross-breeding](#)
- Chicago Tribune: May 28, 2014: [Climate changes push native Montana trout toward extinction: study](#)
- Idaho Statesman: May 27, 2014: [Climate change helps rainbow cross-breed with cutthroats](#)
- Reuters: May 27, 2014: [Climate changes push native Montana trout toward extinction](#)
- Daily Climate: May 27, 2014: [Farewell to the cutthroat trout?](#)
- NBC: May 25, 2014: [Climate Warming Driving Native Trout to Extinction, Study Says](#)
- Flathead Beacon: May 25, 2014: [Researcher Draws Connection Between Climate Change and Harmful Hybridization of Native Trout](#)

Radio

- NPR: Aug 27, 2014: [There's A Big Leak In America's Water Tower](#)
- NPR: May 27, 2014: [Hybrid Trout Threaten Montana's Native Cutthroats](#)

News/Press Release

- May 2014: [Climate Change Accelerates Hybridization between Native and Invasive Species of Trout](#)

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